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Full Name of Author — Nom complet de l'auteur

RUTH ELLEN DUBIN

Date of Birth — Date de naissance

20 AUG 1952

Country of Birth — Lieu de naissance

CANADA

Permanent Address — Résidence fixe

10634 69 AVE., EDMONTON, ALTA. T6H 2C7

Title of Thesis — Titre de la thèse

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Name of Supervisor — Nom du directeur de thèse

Dr. J.R. Nursall

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Social behaviour and ecology of some Caribbean parrotfish (Scaridae)

by

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A THESIS
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(SIGNED) Ruth E. Dubin

PERMANENT ADDRESS:

10634 69 ave
Edmonton, Alta
Canada T6H 2C7

DATED Aug. 7 1981

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Social behaviour and ecology of some Caribbean parrotfish (Scaridae) submitted by Ruth Ellen Dubin in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in ZOOLOGY.

....
Supervisor

Jan O. Murie
Linda Fedigan
W C Mackay
Ellie Prepas

George W. Barlow
External Examiner

Date 7 Aug. 1981

Abstract

Three species of parrotfish (Pisces:Scaridae), *Scarus iserti* (=*croicensis*), *Sc. taeniopterus* and *Sparisoma aurofrenatum*, were studied at Barbados, W.I. to determine how coral cover, competitors (damselfish), food supply, and spawning site suitability affected social systems. An inshore area (< 200 m from shore) had abundant, patchy food, numerous damselfish and heterogeneous coral cover. A second, 500 m offshore, was similar but had less food. Two sites, 600 to 800 m offshore, had few damselfish, low to moderate, evenly distributed food supplies and homogeneous coral cover. The three offshore areas, swept by currents, were better locations than inshore for broadcasting planktonic eggs.

Juvenile *Sp. aurofrenatum* and adults of the three species were more widespread than juvenile *Scarus*, *Sp. viride*, and adult *Sc. vetula*, which were most common inshore. Diurnal, tidal, lunar and seasonal cycles in adult numbers were rare. Juveniles recruited year-round, with peaks from June to September when near-shore currents and water temperature increased.

Juveniles and the dull-coloured initial phases (Iph - mostly females) were less evenly distributed and had more associations with particular coral types than brightly coloured terminal phase (Tph) males. The damselfish, *Eupomacentrus planifrons*, excluded juveniles and Iph from staghorn coral, but not Tph or *Sc. vetula*. The three species did not subdivide space or differ in substrate associations.

Interspecific aggression occurred rarely, and heterospecific groups were common.

Residents and transient intruders were identified. Offshore, males resided for up to two years (one year in *Sc. iserti*) and on disappearing, were rapidly replaced by intruders. Inshore, most fish resided temporarily (two months), varied more in size and were not immediately replaced. Tph males may dwell inshore before becoming intruders offshore. Transition from Iph to Tph colours was rapid (< 1 week) and only partially controlled socially.

Social systems inshore and offshore differed. Offshore, males patrolled stable, contiguous territory borders, excluded only conspecifics and enclosed female harems. Iph fish formed size-dependent dominance hierarchies, but excluded like-sized fish. Inshore, Tph *Sc. iserti* and *Sp. aurofrenatum* had loosely packed, overlapping, highly variable, unpatrolled boundaries and no harems. Some resident Tph *Sc. taeniopterus* perhaps had harems. Tph *Sp. aurofrenatum* inshore shared space temporarily, as did newly transformed *Sc. taeniopterus*, perhaps to enhance feeding success. Tph *Sc. iserti* tolerated most overlap with other males. Territory size was unrelated to fish size or food supply, but decreased where intruders were abundant.

Each species allocated time differently. *Sc. iserti* fed most, *Sp. aurofrenatum* least. All Tph fed less and were more aggressive than Iph. Males offshore chased Iph more than inshore. *Scarus* Tph chased Iph more than *Sp. aurofrenatum*, reflecting higher proportions of Iph males. *Sp. aurofrenatum* and *Sc. taeniopterus* showed the most border defence. Low aggression in *Sc. taeniopterus* was related to its early morning spawning. High damselfish densities resulted in increased sitting by fish but were not responsible for social system differences. Species overlapped extensively in grazing habits. All spawned regularly offshore, rarely inshore.

Intense male-male competition for space, permanent territoriality and harem formation were responses to good spawning sites. Sub-optimal inshore areas were inhabited by males incapable of holding space offshore, or by fish exploiting abundant food before migrating elsewhere to spawn. Interspecific competition for food or space did not occur. Food may not be limiting. Space, defended primarily for spawning purposes, limits only other conspecifics. Behavioural flexibility may account for the success of parrotfish in widely varying reef environments.

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I. Introduction

The study of social systems lies at the interface of ethology and ecology. Much as Wilson (1975) predicted, interest in how animals space themselves relative to needed resources like food and shelter, or other organisms, either competitors or mates, has blossomed in recent years. Such factors are of major importance in influencing social structures within populations (Brown, 1964; Orians, 1969; Brown and Orians, 1970; Emlen and Oring, 1977). These in turn affect the ecology of the species and its community. Territoriality can limit population density (Brown, 1969; Clarke, 1970; Krebs, 1971; Larson, 1980c). Interspecific aggression is a form of competition for food or shelter (Cody, 1969; Myrberg and Thresher, 1974). Social interactions such as cleaning symbioses and interspecific territoriality can act to structure communities (Slobodkin and Fishelson, 1974; Sale, 1978b; Williams, 1980).

Coral reef fish have provided a rich arena for such investigations. Their great range of form, colour and size attracts researchers, and their conspicuousness in clear, warm, tropical waters facilitates field studies. The high species diversity on reefs makes questions concerning resource sharing by closely related species particularly pertinent. Recent reviews of reef fish (Ehrlich, 1975; Reese, 1978; Sale, 1978c, 1980; Keenleyside, 1979) have outlined the diversity of their social structures and inter-relationships. However, our knowledge is curtailed by the short-term nature of many studies, and the lack of detailed autecological work. The damselfish (Pomacentridae) are one exception; this group has received more notice than any other, both because they do well in aquaria, and because their aggressive responses to other organisms, including divers, attract attention. (See Emery, 1973; Sale, 1978c, 1980; Thresher, 1976a, 1977a, 1978b, 1979b; and Williams, 1978, 1979, 1980 for further references.)

The wrasses (Labridae) stand next to the damselfish in popularity with biologists (Randall and Randall, 1963; Feddern, 1965; Roede, 1972; Robertson, 1972, 1973; Reinboth, 1973; Warner, 1975a and later papers; Thresher, 1979a). These ubiquitous omnivores, along with their herbivorous relatives, the parrotfish (S.O. Labroidei, Family Scaridae), have attracted notice because of their predisposition for protogynous hermaphroditism (Reinboth, 1962, 1968, 1975; Choat, 1966, 1969) and the fact that sex reversal is sometimes under social control (Robertson, 1972, 1973). A certain terminology has built up to deal with the bewildering array of sexual types in these groups (Warner and Robertson, 1978). Most fish are born as females and change sex at a later date to become *secondary* (2°) males. Species which have only 2° males are *monandric*. Some species possess both 2° and 1° males, i.e. males that are born as such (*gonochorists*). These species are termed *diandric*. Sexual dichromatism adds to the confusion, particularly because hermaphrodites and gonochorists adopt the same guises. Females and young males are dull-coloured, and are said to be in the *initial phase* (Iph). Larger, older males, both 1° and 2°, develop flamboyant colours (see Plates 2 to 6), and are in the *terminal phase* (Tph). Sex and colour change are often, but not always, closely linked. Both Iph and Tph males are sexually active. Tph males generally spawn in pairs with one female at a time, while Iph males do so in groups (Randall and Randall, 1963; Feddern, 1965; Choat, 1966; Reinboth, 1973). Some Iph males interfere with pair spawnings as well (Warner et al., 1975). Parrotfish spawn pelagically, producing planktonic eggs (Winn and Bardach, 1960; Randall and Randall, 1963). There is no parental care. Males are polygamous, females apparently spawn only once in one day (Warner and Hoffman, 1980a,b).

Parrotfish have been a taxonomically difficult group due to their sexual dichromatism and lack of morphological variation. Iph and Tph conspecifics were usually classified separately. With the advent of SCUBA gear, biologists began observing different colour phases together in natural populations and were able to condense the species lists (Brock and Yamaguchi, 1954; Gosline, 1955). Winn and Bardach (1957, 1960) observed spawning behaviour and feeding aggregations, and induced colour change by testosterone injections to properly classify four Caribbean species. The efforts of Schultz (1958, 1969), Randall (1963b, 1965a, and later papers), and Rosenblatt and Hobson (1969) have done much to reduce the confusion. At present, the family consists of some 68 species (Schultz, 1969), divisible on the basis of jaw and dental morphology into two subfamilies, the Scarinae (three genera) and the Sparisomatinae (seven genera). There are 14 species known from the Caribbean. Six are scarinines (genus *Scarus* - abbreviated as *Sc.* in the text to follow) and the rest are sparisomatinines (genera *Sparisoma*- abbreviated as *Sp.* in the text to follow, also *Nicholsina*, and *Cryptotomus* which were not considered here).

This colourful and attractive family demonstrates some interesting biological features. Scarinines secrete a mucous envelope at night from an opercular gland (Winn, 1955; Casimir, 1971). The mucus, which may be toxic (Cameron, 1976), protects quiescent fish from nocturnal predators (Winn and Bardach, 1959). Sunrise and sunset migrations between day-time feeding areas and night-time sleeping spots have been observed in many locations (Winn et al., 1964; Hobson, 1972, 1973; Collette and Talbot, 1972; Ogden and Buckman, 1973; Dubin and Baker, 1981). Parrotfish appear to be entirely diurnal (Starck and Davis, 1966), and probably possess colour vision (Munz and McFarland, 1975).

Parrotfish exert an impact on coral reefs as a result of their feeding habits. With their beak of coalesced teeth and pharyngeal mill, they browse on marine macrophytes, and graze the surfaces of coral rock, removing filamentous and endozoic algae (Randall, 1963c, 1967, 1974; Ogden and Lobel, 1978). Their grazing is sufficiently intense to significantly reduce fleshy algae and macrophytes on and around reefs, and to promote the growth of reef-cementing coralline algae (Randall, 1961c, 1965b, 1974; Bakus, 1966, 1967; Vine, 1974). Their suppression of filamentous algae apparently improves the survival of coral recruits, and enhances the diversity of benthic organisms (Birkeland, 1977; Potts, 1977; Brock, 1979). As they scrape coralline surfaces, parrotfish ingest a considerable amount of calcium carbonate, and show adaptations for metabolizing it (Fontaine et al., 1973; Smith and Paulson, 1975). Much of this reef material is excreted as sediment, and parrotfish are significant agents of bioerosion on reefs (Bardach, 1961; Randall, 1963c; Gygi, 1975; Frydl and Stearn, 1978; Frydl, 1979; Scoffin et al., 1980). They are important food fish to natives of coral reef areas, and are often implicated in outbreaks of ciguatera poisoning (Chungue et al., 1977).

The evolution of protogynous hermaphroditism and sexual dichromatism in labroid fishes has been attributed to sexual selection, brought about by female choice of large, brightly coloured males (Robertson and Choat, 1974; Warner, 1975b, 1978; Warner et al., 1975). A fish that reproduces as a female while small, then changes sex later to reproduce as a male, has a selective advantage over a gonochorist of either sex. The existence of both 1° and 2° males may be a genetic polymorphism, controlled by local population size (Warner et al., 1975, Warner and Hoffman, 1980a, 1980b). A species' social organization may also determine its sexual makeup (e.g. monandric or diandric; many or few Iph males; Robertson and Warner, 1978). Social structures are in turn determined by resource abundance and distribution patterns (Warner, 1979). Thus, species which have strict haremic systems, where one male dominates and spawns exclusively with several females, are expected to be monandric. Species with looser social systems, where individual recognition is less likely, would possess Iph males.

Robertson and Hoffman (1977) have attempted to show a positive relation between the looseness of the mating system, i.e. the extent that females can choose their mates, and the degree of sexual dichromatism. Their arguments are based on the supposition that bright male colours function entirely to attract females, and are clearly premature. Thresher (1979a) has pointed out that monochromatism can be interpreted as an adaptation to a specialized life style (e.g. cleaning other fish), and that bright male colours also play a role in male-male interactions. He has shown that monandry, monochromatism and strong harem formation are not always closely linked. All the authors involved with such questions have voiced the sentiment that more species must be studied to confirm their generalizations.

Robertson and Warner (1978) attempted to test their ideas on the linkage between social structure and sexual systems in a survey of Caribbean parrotfish. They showed that all *Sparisoma* species were monandric, while *Scarus* possessed variable numbers of 1° males. They found some agreement with their hypothesis that strongly haremic species should lack Iph males, but other species fit their scheme less well. Their major problem was a lack of solid information on social structures, which can be highly variable. For example, in *Sc. iserti* (formerly *croicensis*; Randall and Nelson, 1979), young fish form small, stationary foraging groups. Larger ones join massive, roving feeding aggregations. Sexually mature Iph females live within harems controlled by a Tph male (Buckman and Ogden, 1973; Ogden and Buckman, 1973; Warner and Downs, 1977). Elsewhere in the Caribbean, *Sc. iserti* is not haremic, but forms leks (Barlow, 1975). The life history stages of other Caribbean scarids are very poorly known, and one of the aims of my thesis was to fill in this gap.

While social system variability is usually ascribed to differences in resource abundance and distribution patterns, these ideas have not been tested on reefs. My primary goal was to investigate the effects of differences in ecological factors on social systems of selected Caribbean parrotfish by carrying out a correlative study in several reef locations. While experimental interventions are useful for testing hypotheses, they are not the *sine qua non* of scientific activity (Chitty, 1967), and would in fact have been premature in the poorly known system under surveillance. The correlative approach, when combined with careful and quantitative behavioural measurements, can be a productive means of testing sociobiological theories (Gould, 1980).

The distribution and abundance of food is usually considered to be the ultimate determinant of labroid social systems with defence of space appearing only when resources make it economically feasible (Choat and Robertson, 1975; Barlow, 1975; Robertson and Warner, 1978; Thresher, 1979a; Warner, 1979). However, the underlying assumption that these fish are actually competing for food has never been tested. Likewise, no one has looked at social systems over a range of food levels. Many reef fish space themselves in relation to coral cover (e.g. Sale, 1972a, 1972b; Choat and Robertson, 1975; Fricke, 1979). There is evidence, however, to counter the wide-spread belief that cover is in short supply on reefs (Robertson and Sheldon, 1979). Territorial aggression by other species affects social organization by forcing fish to form schools in order to feed (Barlow, 1974b; Robertson et al., 1976). The effect of predators is much more difficult to assess (Luckhurst, 1977; Sale, 1980), and may, in fact, be of relatively little importance to the species studied here (Williams, 1980). Finally, spawning site suitability should be considered, since many reef species are apparently quite selective in their spawning locations (e.g. Johannes, 1978), and the possibility that mates may be a defended resource has been raised (Emlen and Oring, 1977; Thresher, 1979a). I set out to measure each of these factors at several reef locations at the same time that I determined the social structure and behaviour of three parrotfish species.

My approach was a compromise between broadly based but necessarily superficial surveys of many species (e.g. Jones, 1968; Choat and Robertson, 1975; Robertson and Warner, 1978), and more detailed investigations of one species (e.g. Buckman and Ogden, 1973). Because the two common Caribbean genera, *Sparisoma* and *Scarus*, apparently show rather different social behaviours, with the former more solitary than the latter (Winn and Bardach, 1960; Barlow, 1975), I resolved to choose one species from each for comparison. Of the two *Sparisoma* species common in my study areas (see Chapter 4), one, *Sp. viride*, was too large and vagile to be observed profitably. Therefore I chose the other, *Sp. aurofrenatum*, the redband parrotfish, as the *Sparisoma* representative. Since the data base on *Sc. iserti* (=*croicensis*), the striped parrotfish, was already relatively large in other Caribbean locations, I decided to study it, along with its poorly known and very closely related congener, *Sc. taeniopterus*, the princess parrotfish.

In addition to determining how the ecological factors chosen varied from location to location, I generated hypotheses concerning how each factor should affect social behaviours (Chapter 3).

I was also concerned with gathering baseline data on population processes in parrotfish (Chapter 4). A controversy has arisen recently as to whether reef fish communities are determined by stochastic processes (Sale and Dybdahl, 1975, 1978, Sale, 1977, 1978b) or competitive interactions and niche specialization (e.g. Smith and Tyler, 1972; Smith, 1978). I had no intentions of attempting to resolve this debate. However, information on population stability and juvenile recruitment is very limited, especially from long-term studies, yet is crucial to understanding how reef communities function (Sale, 1980). The major role played by parrotfish in the reef ecosystem necessitated an improved understanding of their population cycles.

The importance of interspecific competition among closely related species has been investigated in the damselfish (Sale, 1974, 1975, 1978a, 1978b, 1979; Itzkowitz, 1977b; Robertson and Lassig, 1980; Waldner and Robertson, 1980), but not in the parrotfish. While often considered a specialized group (Hobson, 1974, 1975; Ogden and Lobel, 1978), their lack of morphological variation (Schultz, 1958; Randall, 1963b) hints that they may be very similar competitively. In Chapter 5, I consider the question of competition for space by carrying out an analysis of their spatial distribution patterns. In a later chapter (7), competition for food is discussed. Substrate variables might also affect species' distributions (e.g. Luckhurst and Luckhurst, 1978a; Fricke, 1979), and this aspect is considered as well in Chapter 5. Determining what controls a species' distribution in space is a requisite of understanding what limits are placed on its social system.

The degree to which animals remain in particular locations (i.e. site-attachment) may depend on their social status. Individuals pass through different behavioural states as part of their life cycle. Parrotfish life history is complicated by sex and colour changes, which are still poorly understood. The amounts and mechanisms of individual turnover within and between groups must be elucidated to learn how social groupings are maintained. Chapter 6 deals with these problems, and compares the population structure and processes of individual turnover for species inhabiting different areas.

In Chapter 7, quantitative information on feeding, reproduction, and social behaviour is presented in the form of activity (time) budgets. Use of space is also considered there. The overall goal of this section is to characterize each species' social system, determine the extent of its variability under different ecological regimes, and, through the analysis of time budgets, pinpoint the priorities of the fish inhabiting each ecological zone (e.g. feeding, reproduction, etc.). As well, I consider whether species use space and food in different ways. In a concluding chapter (8), I discuss which ecological factors have the greatest effects on parrotfish social behaviour. I also explore the impact of social systems on population stability. The three species chosen for intensive study are compared in order to elucidate their different adaptations for sharing space and food in the complex and variable reef environment.

II. Methods and study areas

A. Location and time span of studies

I studied parrotfish social behaviour at the Bellairs Research Institute of McGill University on Barbados (13° 10′ N, 59° 30′ W), a small coral-capped island lying in the North Equatorial Current approximately 140 km east of the Lesser Antilles in the southern Caribbean (Figure 1). The distribution and species composition of Barbados reefs were described by Lewis (1960a). Stearn et al. (1977) mapped the ecological zones in the vicinity of Bellairs, where my work was carried out.

The study ran from May, 1976, to August, 1977, and from May, 1978, to July, 1979. Owing to a diving injury no observations were made in May, 1977. In August, 1979, I studied *Sp. aurofrenatum* in the San Blas Islands of Panama (9° 39′ N, 78° 45′ W) on two patch reefs near Porvenir Island (Robertson and Glynn, 1977).

Four permanent study sites were set up in Barbados over the course of the project (Figure 2). I chose the study sites because they had abundant parrotfish, represented different coral zones, and were relatively free of interference from local fishermen. Although some trap, line, and spear fishing occurred on the sites in 1976-7, fishermen kindly agreed to stay away in 1978-9.

Each site consisted of a rope grid of 10 m by 3 m quadrats laid on the bottom. Coloured tapes were attached to

Figure 1. Location of Barbados and study areas on the west coast.

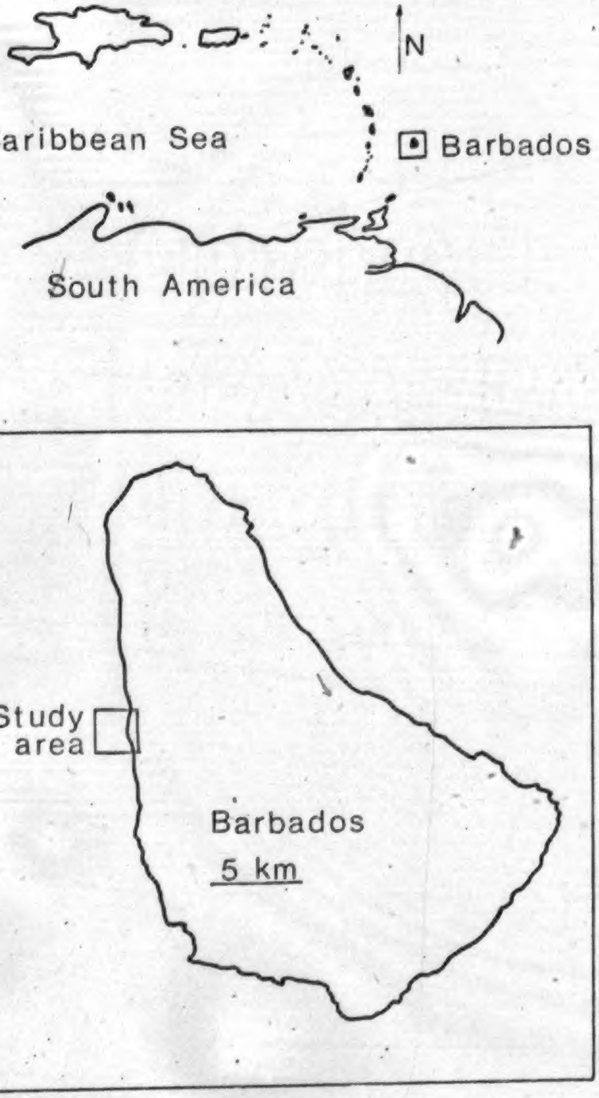
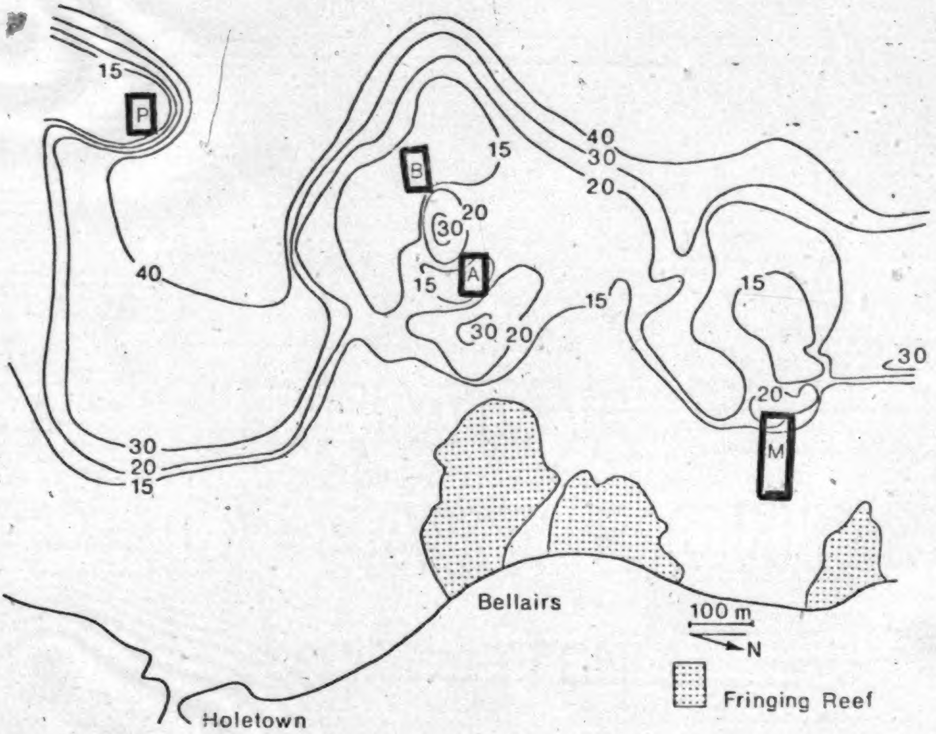

N
Caribbean Sea
Barbados
South America
Study area
Barbados
5 km

Figure 2. Bathymetry of the coast near Bellairs Research Institute showing locations of study sites M, A, B and P (from Stearn et al., 1977 and Richards and Bird, 1970). Depths are in metres.


15
P
B
15
40
30
20
30
20
A
15
40
15
30
20
15
30
20
M
30
20
15
Bellairs
Holetown
100 m
N
Fringing Reef

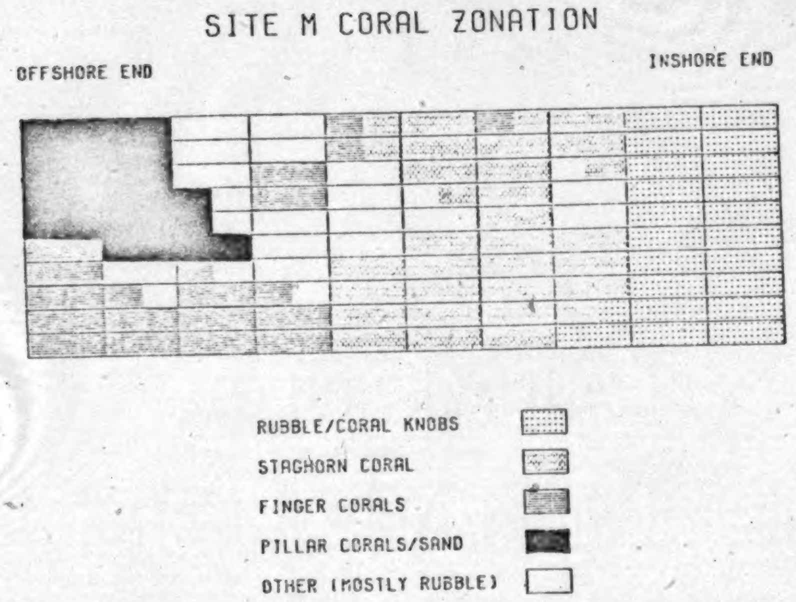
the borders of each quadrat to allow identification of the diver's position in the grid using Cartesian coordinates. A brief description of each study site follows.

Site M

Site M, known locally as the Moorings, lay inshore, ca. 200 m from the beach (Figure 2). Forty quadrats were established in June, 1976, for a preliminary study and it was enlarged in August, 1976, to 100 quadrats. Its final overall dimensions were 30 m by 100 m (3000 m^2). Site M contained a mixed coral community (Lewis, 1960a) which sloped gradually seawards from 6 m to 18 m in depth. At its western (seaward) end it joined a series of circular hollows that may have formed by solution during Pleistocene low sea levels (Stearn et al., 1977). It had the most heterogenous cover of all the study sites, and contained four well-delineated coral zones, in increasing distance from shore (Figure 3, zones described by Stearn et al., 1977):

1. The rubble zone (Plate 1A) consisted mainly of coral rubble, sand, small coral knobs (*Diploria strigosa* and *Montastrea annularis*), and some finger corals (*Porites porites* and *Madracis mirabilis*).
2. The staghorn coral zone (Plate 1B) consisted of large stands of *Acropora cervicornis*, a sharply pointed, branching coral, together with some massive, clubbed heads of *Montastrea annularis*.
3. The finger coral zone (Plate 1C) covered parts of the reef that sloped gently from 10 m to 15 m. It consisted

Figure 3. Coral zonation at site M.



of delicate branches of *Madracis mirabilis*, with some *Porites porites*, and rubble.

4. The pillar coral zone (Plate 1D) covered the steeper slopes at the seaward end of site M. It consisted of massive corals (*Montastrea annularis*, *Diploria strigosa*, and *Siderastrea* spp.), many of them dead, and sand.

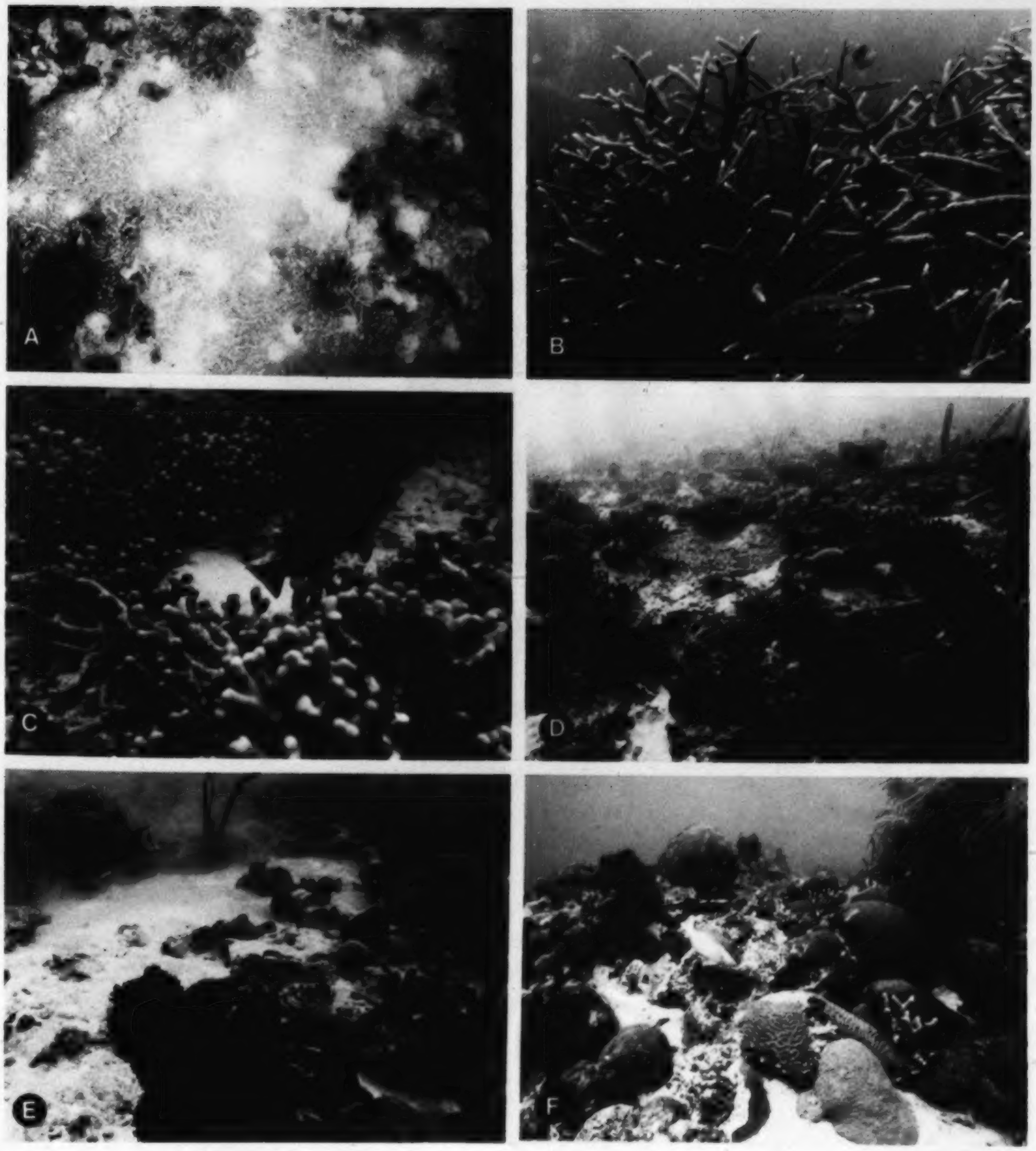
In addition, some areas at site M consisted entirely of coral rubble, which may have been created by anchor chains from boat moorings that had been removed.

Horizontal visibility at site M varied from 30 m to less than 3 m during periods of heavy rainfall or winter swells, and averaged 10 to 15 m. The temperature at all depths and study sites varied from 29.5° in September to 26.5° in March (Sander and Steven, 1973).

Site B

Site B (Figure 2), known locally as the Bank Reef, was chosen to represent an offshore area. Site B lay 600 m offshore at a depth of 13 m on the ridge top of a barrier reef which parallels most of the west coast (Macintyre, 1967). It was established in December, 1976 and contained 50 quadrats, with approximate total dimensions of 30 m by 50 m. Due to an error in laying lines some quadrats were wider than 3 m. These were later measured, both underwater, and with a planimeter on photographs. The actual area of site B was 1800 m². The barrier reef is covered mostly by evenly distributed dome-shaped corals (*Diploria* spp., *Montastrea annularis*, *M. cavernosa*, and *Siderastrea siderea*), soft

Plate 1. Examples of coral types:
A: rubble zone with sand, coral rubble, and small knob-like coral heads.
B: staghorn coral zone of *Acropora cervicornis*.
An Iph *Sc. iserti* swims in the foreground;
C: finger coral zone showing *Porites porites*. *Madracis mirabilis* is similar, but smaller and finer. An Iph *Sp. aurofrenatum* is visible;
D: pillar coral zone with massive corals and sand;
E: coral cover type on barrier reef near site B;
F: denser coral cover on barrier reef site P.


A
B
C
D
E
F

corals, sponges and sand (Ott, 1975; Plate 1E). A trough up to 40 m deep separates this offshore reef from inshore communities in some places, but inshore and offshore regions are continuous near the circular hollows mentioned above. Site B was subject to heavy swell action from December to April. Visibility averaged over 20 m, and ranged from 12 m to 30 m.

Site P

Site P (Figure 2), known locally as the Parasail Reef, also lay offshore, and was chosen primarily to act as a control for site B. No experiments, collections, or marking of fish occurred there from 1977 on. Consisting of 50 quadrats (30 m by 50 m, 1500 m²), it was established in May, 1978. Site P lay southwest of site B some 800 m from shore at 13 m depth on a separate lobe of the barrier reef. Coral composition resembled that of site B, but the corals were more densely packed at site P and gorgonians (sea fans and whips) grew more luxuriantly there (Plate 1F). It lay close to the shoreward and northward slopes of the barrier reef. The visibility averaged over 25 m, except during winter swells, when it fell to 12 to 15 m.

Site A

Site A (Figure 2), the Martlet or Acropora Reef, was established in May, 1979, for comparative purposes when I discovered that numerous adult parrotfish immigrated there at sunset (Dubin and Baker, 1981). It also consisted of 50 quadrats (30 m by 50 m, 1500 m²). Site A lay 450 m offshore at 15 m to 20 m depth on a narrow ridge between two circular hollows, which adjoined the offshore barrier reef. Coral cover resembled that at site M, although it was less heterogenous, and lacked the low relief rubble and small knob coral zone (Plate 1a). Staghorn coral (Plate 1b), finger corals (Plate 1c), and some rubble were most common. Pillar corals (Plate 1d) appeared on its sloping seaward end. Site A was deep enough to be protected from heavy wave action, but light levels were lower there and visibility ranged from 10 m to 15 m.

B. Measurement of ecological variables

Cover

In order to assess bottom cover at sites B and P, I photographed each 30 m² quadrat using a Nikonos camera fitted with a Nikkor 15 mm lens. I could fit one entire quadrat into the picture by hovering 6 to 8 m from the bottom. An assistant placed a 1 m² grid in the centre of the quadrat for scale, placed a pole to mark one end of the quadrat, and sat at the other end holding a slate to identify it. I used Kodak Tri-X (ASA 400) black and white film at site B, and Ektachrome (ASA 200) colour slide film at site P. Natural light levels were adequate on bright days. I made 20.3 by 25.4 cm prints of the site B pictures, and projected the site P slides on a screen. The percent cover in each quadrat by sand and rubble was estimated by counting 100 to 125 random points (Bohnsack, 1979). A more involved analysis of the coral species present was unwarranted, since species composition was similar at the two sites, coral cover was relatively homogeneous, and it had already been well described (Ott, 1975).

Owing to lower water clarity at site M, I was unable to photograph each quadrat entirely, so took 300 black and white pictures of 1 m² subquadrats. The percent cover in each quadrat by sand and rubble, small knob-like heads, finger corals, staghorn coral, and massive coral heads was measured by counting squares in an overlaid grid. The photographic analysis agreed well with my subjective estimate of coral type (Figure 3).

No photographs were taken at site A because of time limitations. However, I prepared a map of substrate type and visually estimated cover by sand and rubble, finger corals, staghorn coral and massive coral heads.

Food supply

The feeding habits of parrotfish have been the subject of controversy, some authors considering parrotfish omnivores (Al-Hussaini, 1945, 1947), feeders on live corals (Gohar and Latif, 1959; Hiatt and Strasbourg, 1960), or on macrophytes and filamentous algae (Randall, 1967, 1974; Vivien, 1973; Smith and Paulson, 1974; Choat and Robertson, 1975). Although they lack lichenase or cellulase in their guts, grinding by their pharyngeal mill may expose plant cells to digestion by amylases (Gohar and Latif, 1960; Ogden and Lobel, 1978). It seems clear that their feeding habits may vary considerably among geographic locations but that parrotfish are primarily herbivorous. Macrophytes were uncommon on Barbados' west coast (Lewis, 1960a), and scarids there grazed the surfaces of dead coral and sand, removing filamentous red, green and blue-green algae, detritus, and small invertebrates (Vivien, 1973; Parrish and Zimmerman, 1977; Brock, 1979; Scoffin et al., 1980). Only one species, *Sp. viride*, grazed live coral, but did so rarely (Gygi, 1975; Frydl, 1979; pers. obs.).

I estimated food supply at each site by measuring the biomass of filamentous algae that settled and grew on porcelain bathroom tiles (232 cm^2) over 21 days (Vine, 1974). Twenty-four tiles were placed matt side up once a month at sites M, B, and P from September, 1978, to June, 1979, and in June, 1979 at site A. All samples in February, 1979, were lost in a severe storm. Care was taken to avoid overhangs or the territories of herbivorous damselfish whose aggressive and "farming" behaviours increase reef algal biomass (Vine, 1974; Brawley and Adey, 1977; Lassuy, 1980; Lobel, 1980). Tiles were placed on blocks to prevent them from being smothered by sand.

I estimated biomass on both grazed and ungrazed tiles. Half of the tiles were protected from grazing within cages of 19 mm diameter wire mesh. This mesh size was sufficient to exclude both fish and invertebrate herbivores with the exception of small snails and juvenile parrotfish. I excluded juvenile parrotfish by raising the cages 0.75 m above the sea floor and lining the bottom of the cage with black plastic. Juveniles did not swim more than a few centimeters above bottom (Itzkowitz, 1974). Snails, encountered rarely, were removed.

Once an algal mat appeared on the exposed tiles they were grazed, and were covered with parrotfish beak marks upon collection. I had no reason to believe that the exposed tiles were grazed more or less heavily than the surrounding substrate.

Material that had grown on each tile was scraped off with razor blades, macroscopic invertebrates were removed, and the calcium carbonate sediment was dissolved in dilute HCl (Vine, 1974). Samples were filtered onto previously dried and weighed filter papers, dried overnight at 80° C, and weighed to 0.001 gm.

Biomass of algae from caged tiles, i.e. tiles protected from grazing, represented the potential food supply of an area. It estimated the food that would have been available if no grazing were occurring, and was intended to reveal differences at sites due to depth, nutrients, light and factors other than grazing. Biomass on tiles exposed to grazing estimated the actual food supply of an area, the amount available to a fish at any one time. Taken together the two measures could be used as a rough indicator of an area's food supply. Although biomass estimates ignore algal species composition or food quality differences among study areas, they allow a ranking of areas in order of food abundance. A detailed study of parrotfish feeding ecology, while much needed, was beyond the scope of this study.

Competitors

To assess the densities of possible parrotfish competitors, I counted all visible fish (except parrotfish, whose numbers were estimated separately). Surveys were made on two occasions 6 to 18 months apart at sites M, B and P, and once at site A, by two observers swimming side by side up and down the study area lanes. Emphasis was placed on counting herbivorous damselfish which are known to exclude parrotfish from their territories (Vine, 1974; Robertson et al., 1976). The most common species, *Eupomacentrus planifrons*, cultivates rich algal lawns which are an attractive food source to other herbivores (Robertson et al., 1976; Kaufman, 1977). This visual survey underestimated very small fish (e.g. Gobiidae, Blenniidae and Clinidae), and secretive species (Scorpaenidae and Muraenidae). However it gave good estimates of the conspicuous fish most likely to compete with parrotfish: Pomacentridae and Acanthuridae. Invertebrate herbivores were not counted. Conch (*Strombus* spp.) were uncommon at all study sites. The sea urchins *Tripneustes esculentus* and *Echinometra* spp. were rarely seen. While the urchin *Diadema antillarum*, reaches great densities on the fringing reefs of Barbados (Stearn et al., 1977), it was not abundant at my study sites.

Abiotic variables

Tidal range in Barbados is only 1 m (Lewis, 1960b), but I noted tide height (i.e. high, midway, low) and movement (ebb, slack, flow) based on tables supplied by the Meterological Services of the Grantley Adams International Airport. Temperature was measured each week at a depth of 10 m with a hand-held thermometer.

I paid particular attention to factors which might influence spawning behaviour. Researchers have noted that fish producing planktonic eggs spawn near deep, seaward reef slopes or promontories, often in the same spot for many years (Randall and Randall, 1963; Robertson and Choat, 1974; Choat and Robertson, 1975; Robertson and Hoffman, 1977; Colin, 1978; Colin and Clavijo, 1978; Johannes, 1978; Lobel, 1978; Thompson and Munro, 1978; Fischer, 1980; Jones, in press). Areas that are swept by currents are often chosen for spawning (Johannes, 1978; Warner and Hoffman, 1980b) allowing fish to broadcast their eggs to oceanic waters where the larvae develop, or avoid egg predators which hover over the reef, (Johannes, 1978; Barlow, 1980). Reef fish may select spawning sites near points where current gyres will carry eggs off the reef and return pre-settlement larvae to it (Jones, 1968; Sale, 1970; Emery, 1972; Leis and Miller, 1976; Johannes, 1978). I subjectively monitored the direction and intensity of any currents, and noted each site's proximity to offshore waters, reef slopes and promontories.

C. Identification of individuals

Identification of individuals is necessary in most behavioural studies. Most terminal phase males, and some initial phase fish, were recognizable from scars or variations in their markings. This is a commonly used technique (Reese, 1973; Sale, 1974; Williams, 1978; Warner and Hoffman, 1980a). For Tph *Sc. taeniopterus* and *Sc. iserti* (Plates 2, 3), I used the shape of the blue bands between the eyes, and the pattern of orange margins and spots on the tail. For Tph *Sp. aurofrenatum* (Plate 4), I used the shape of the black and yellow post-opercular spots (see also Bohlke and Chaplin, 1968, or Chaplin and Scott, 1972, for details of colour patterns). I sketched an individual's features carefully on first sighting, and carried these sketches with me for future reference. Additional sketches were made occasionally to verify identifications.

Fish at sites M and B were captured in small Antillean fish traps (Munro et al., 1971), transferred at depth through a sliding door into a soft mesh bag, and marked by subcutaneous injections of acrylic paint (Thresher and Gronell, 1978). The marking procedure minimized the time fish spent in captivity, and prevented overexpansion of the gas bladder caused by bringing the fish to the surface. I could mark and measure six fish in less than 10 minutes. The acrylic marks were visible from 2 to 3 m away for three to six weeks, and were apparent after six months in hand-held specimens. Early efforts at sewing beads or disc tags into the dorsal musculature failed because tags usually ripped out.

The positions of known individuals within the grid were recorded at each sighting so that disappearances, newcomers or shifts could be discerned. Fish whose territories bordered on each study grid were also identified in this way.

D. Population estimates

In order to measure population composition and fluctuations, I made weekly grid surveys at all sites (twice weekly at site M in 1976; weather and health permitting) by swimming up and down the lanes of quadrats. The species, phase (juvenile, Iph, Tph), and behaviour of all parrotfish encountered were recorded, along with the size and composition of groups. Similar transect surveys have been used by many researchers (Brock, 1954; Bardach, 1959; Bradbury and Goeden, 1974; Rotenberry and Wiens, 1976; Keast and Harker, 1977; Demartini and Anderson, 1980; Hixon, 1980a; Larson, 1980a; Leum and Choat, 1980; Waldner and Robertson, 1980; Birkeland and Neudecker, 1981). Behavioural categories were swimming, feeding on dead coral or sand, sitting (i.e. holding the same position in midwater, or resting immobile against coral heads), and interacting aggressively with other fish. This information was used to complement the more detailed activity budget information (see below). Fish were classed as being in groups when they were feeding or sitting within one to three body lengths from other fish, or were swimming in the same direction. I swam 1 or 2 m above the tops of the coral heads and counted known individuals each time they were seen, on the assumption that multiple sightings were balanced by none for some fish. This assumption appeared to be supported by the data (compare Table 5 with Tables 19 to 21). For example 6.33 Tph *Sp. aurofrenatum* on average were counted at site B. Three to four males had territories completely within the study grid (Table 19), four others overlapped it partially and were seen only sometimes, and 8.2 % of the males sighted were unidentifiable or non-resident.

I watched carefully for juvenile fish during the surveys. They were identified on the basis of colour pattern (*Sp. aurofrenatum* and *Sp. viride*, see Chaplin and Scott, 1972), and size, which was estimated visually at less than 50 to 60 mm standard length. I could not distinguish among the *Scarus* juveniles underwater. The presence of new recruits (fish under 15 mm SL, Leis and Miller, 1976) was noted, and their size estimated relative to the width of my fingers.

Diurnal variations of numbers were investigated by making the survey during each of four time periods: 1 to 2 hours after sunrise, 3 to 5 hours after sunrise, 6 to 8 hours after sunrise, and 9 to 11 hours after sunrise. Thus each time period was sampled once every four weeks at each site, with the order randomized to lessen any confounding effects due to moon phases or tidal cycles. At each survey, I noted the tidal state, water temperature, force and direction of any currents, along with water calmness and cloud cover. No surveys were conducted when visibility fell below 6 m.

These surveys allowed estimates of parrotfish densities and distribution, group composition, behaviour and diurnal or seasonal changes in abundance. They also helped me to detect disappearances or shifts of known individuals. Due to its size, only half of site M was surveyed on each of 58 occasions in 1976-7, and 50 times in 1978-9. The halves were alternated each week. Sites B, P and A were sampled entirely each time. Site B was surveyed 22 times in 1976-7 and 49 times in 1978-9. Site P was surveyed 48 times in 1978-9. Site A was sampled four times in June, 1979 and was excluded from analyses for diurnal or seasonal trends.

E. Behavioural studies

General observational techniques

All observations were made using SCUBA gear at depths of 6 to 25 m. SCUBA diving's major disadvantages are cold fatigue, and limited time due to depth considerations. Each dive lasted from 50 to 120 minutes; I could dive at most three times a day. The total observation time (900 hours) was small compared to many terrestrial studies. However, the fish were nearly always in view, and appeared unconcerned by my presence. My behavioural observations were thus both intensive and reliable. There is no doubt that the fish knew I was there. However, I felt that they rapidly became accustomed to me. By not kicking up sand with my fins, and by hovering 2 to 3 m above and behind the fish, I minimized my effect on their behaviour. Two to 3 m was chosen because fish stopped following me with their eyes at that distance.

Reproductive behaviour

Pair and group spawning were noticeable events that have been well described (Winn and Bardach, 1960; Randall and Randall, 1963; Buckman and Ogden, 1973; Barlow, 1975; Colin, 1978; Robertson and Warner, 1978; Dubin, 1981). I noted all bouts of spawning, but because I could not always predict on what days and where on the reef spawning would occur, my attempts at measuring actual amounts of spawning by specific individuals failed. However, I expressed the total number of days on which spawning occurred in an area as a proportion of the hours of observation spent there during each species' daily spawning period, thus obtaining a rough measure of the amount of reproductive activity for a given species in each area.

Feeding behaviour

To determine whether species differed in food habits, I observed 10 Iph and 10 Tph *Sc. iserti*, *Sc. taeniopterus*, and *Sp. aurofrenatum* at sites M, B and P in 1978. The number of bites on sand, rubble, massive coral heads, branching corals (this included both staghorn and finger corals), and other objects such as sea urchins and gorgonians were recorded during a five-minute period. I could not see what algae the fish were ingesting, and could only infer differences in food intake from differences in the substrates grazed. All feeding observations were made between 0900 and 1600 hours to avoid reductions in feeding activity near dusk and dawn (Dubin and Baker, 1981).

Activity budgets and space utilization patterns

To measure fish activity budgets and space utilization patterns, I used the instantaneous sampling method of Altmann (1974). All such samples were taken between 0800 and 1700 hours, with most between 0900 and 1600 hours. I followed one individual continuously for several five to 25 minute sampling periods (mean = 11.1 minutes) and noted its position and behaviour every five seconds on a map of the grid drawn on a slate or piece of underwater paper. A five-second interval was sufficiently brief to provide an adequate sample in a short time, yet was long enough to allow efficient coding. From 1976 to early 1978 I established the time interval by counting (Nursall, 1981). Later I watched a flashing submersible diode light attached to my mask, or less often watched the second hand of a diving watch. Use of an external timer decreased the variance of the interval between counts and brought it nearer the chosen interval of five seconds (without timer mean interval = 5.8 seconds, $s^2 = 6.6$, $n = 521$; with timer mean = 5.2 seconds, $s^2 = 0.9$, $n = 301$).

I built up a map of space utilization patterns in a study area by sampling all resident terminal phase males at least twice within a two to 10 day sampling period. Due to interruptions in my diving schedule, sampling periods were occasionally longer. In 1976 and 1977 such samples were made at site M and site B at irregular intervals. In 1978-9 I mapped each site at approximately six month intervals. Site B was sampled in May-June , 1978, October-December, 1978 and May, 1979. Site M was observed in July-August, 1978, and January-February, 1979. Site P was mapped in September, 1978, and April, 1979. Site A was sampled once in May-June, 1979. Initial phase fish were too abundant to be completely sampled, so all those residing in subsections of the study grid were observed irregularly in 1976-1977 and once in 1978-1979. Site M Iph were observed in February-March, 1979, site B Iph in December, 1978, and site P Iph in September, 1978. Too few site A Iph were sampled to warrant analysis.

Not all parrotfish were residents of the study areas (see Chapter 6). I followed intruding Tph on a few occasions but their numbers were small. I could only distinguish resident Iph fish by marking, but followed unmarked fish as well. These latter were chosen haphazardly from the study grid.

The information from instantaneous sampling was coded for computer analysis to produce:

1. A map of each individual's home range or territory during each sampling period.

2. The area in m^2 enclosed by each individual's movements during each sample.
3. The percent of time spent in each portion of the territory.
4. The activity budget, expressed as the percent of the total behaviours counted that were made up by a given behaviour.
5. The distribution of particular behaviours throughout the territory.

I paid special attention to aggressive interactions, and tried to identify the individuals involved as well as the intitiator and the level of intensity. A detailed description of the behavioural categories used is found in Chapter 7.

F. Collections and removals

To assess fish sizes and sexual state, and to check my visual estimates of length, I trapped or speared fish intermittently throughout the study. They were weighed and measured, and their gonads were weighed and preserved in Bouin's solution for histological analysis. Most fish were taken from areas near the study grids. However no fish from near site P were collected after 1977.

Intensive trapping and removals of Tph *Sp. aurofrenatum* occurred on one portion of site B in July, 1977. In 1979, five site B Tph males were removed serially from one territory at two to five week intervals, and the time until the next male arrived was measured. Resident fish were captured in traps, measured, and released on sites M and B at intervals of one to eight months. By 1978, I could visually estimate fish size to within 10 mm. Lengths are quoted in millimetres in the text unless otherwise noted, and are given as standard lengths (SL).

G. Computer analysis

I analysed data on the computer with statistical packages such as SPSS and BMDP. The statistical tests used are described in Siegel (1956), Sokal and Rohlf (1969), or Snedecor and Cochrane (1980). Values quoted for statistics are shown with the degrees of freedom in parentheses. I wrote computer programs in FORTRAN and WATFIV to calculate activity budgets and produce territory maps. A SURFACE graphics package from University of British Columbia was implemented to draw three-dimensional perspective views of space utilization patterns. Specific details of analyses are given in pertinent chapters. Because of the large quantity of data involved, raw data are not always presented in the thesis, but rather have been stored on computer tape, copies of which are available on request from the author.

III. Ecological variables

Analysis of coral cover, food supply, competitors and spawning suitability allows characterization of the ecological situation at each study area. It also permits setting up specific hypotheses concerning the effect that each factor should have on parrotfish social behaviour.

A. Cover

The four study areas fell into two groups with very different coral types: sites M and A on the one hand, and sites B and P on the other (Table 1). Sites M and A had staghorn corals, finger corals, rubble and some large coral heads. Site A lacked the knob-like coral heads that were present in the shoreward end of site M. Site M had less coral cover per quadrat than site A, but this was partly an artifact of its greater size and overall heterogeneity.

Finger corals, staghorn coral and small knob-like coral heads were scarce at sites B and P. These two barrier reef sites had clumps of coral and other sedentary organisms interspersed with sand. Hemispherical coral heads comprised the great majority of the zoobenthos; sponges; gorgonians, sea anemones and antipatharians made up only 7 % of the bottom (Ott, 1975). Site P had denser coral cover, and a lower variance in percent cover among quadrats than did site B (Table 1). Assuming no differences in sites B and P in the percentage of each coral colony that was dead, then site P, with more corals, had more total dead coral surface - a

Table 1. Average percent cover by sand and rubble, staghorn coral, other substrate types, finger corals, and small knob-like coral heads at each study site. Other substrate types include dome-shaped coral heads, gorgonians and sponges of which coral heads are the most abundant. Total coral cover and percent dead coral[1] are also shown. Values are mean per quadrat ± standard deviation. n: number of quadrats.

	Site M n = 100	Site A n = 50	Site B n = 50	Site P n = 50
Sand and rubble:				
	39.5±21.1	43.6±27.1	42.2±14.9	25.1± 6.1
Coral cover:				
Staghorn coral	18.3±23.2	48.0±29.5	0.0	0.0
Other:dome corals	6.2±12.0	5.4±11.5	57.8±14.9	74.9± 6.1
Finger corals	25.6±21.3	3.6± 5.7	0.0	0.0
Knob-like corals	10.4±14.2	0.0	0.0	0.0
Total coral cover:				
	60.5±21.5	56.4±27.0	57.8±14.8	74.9± 6.1
Percent dead coral[1]:				
	15.1± 5.4	14.1± 6.8	10.4± 2.7	13.5± 1.2

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[1] Calculated using dead coral = 18 % of total coral cover at sites B and P (Ott, 1975), and dead coral = 25 % of total coral cover at sites M and A.

major grazing substrate of Barbados parrotfish (see Chapter 7) - than site B. I could not distinguish dead and live coral reliably in my photographs of sites B and P. However Ott (1975) found that 18 % of the total coral was dead at a depth of 12 m on the barrier reef. Twenty-five percent of the total coral cover at site M was dead. Ott (1975) also found that dead coral increased in staghorn and finger coral zones. Thus site B had the least dead coral cover of all, and sites M and A had the most, slightly more than site P (Table 1).

An analysis of photographs has certain drawbacks. All measurements of percent cover are made from planar projections of the extremely complex reef surface. Actual surface area of reefs may be up to 15 times the planar surface area (Dahl, 1973). Measurement of true surface area is both approximate and complex, even on a much smaller scale than that of the present study (Dahl, 1973; Stearn et al., 1977; Birkeland and Neudecker, 1981). Comparison among study areas is difficult because branching corals like those at sites M and A possess a greater actual surface than do hemispherical corals like those at sites B and P (Dahl, 1973). Nevertheless, differences in parrotfish behaviour which were related to coral cover type, would be expected to mirror the division of study areas into two groups: sites M and A with branching corals, and sites B and P with hemispherical corals.

B. Food supply

Figure 4 shows the average dry weight (grams per 100 cm^2) of organic matter growing in 21 days on porcelain tiles, averaged over months. Variations from month to month were inconsistent and no seasonal trends were visible.

As expected, the biomass was greater on caged tiles than on those exposed to grazing. Species composition also differed. Caged plates were covered with a 0.5 to 1.0 cm thick layer of filamentous algae. Exposed tiles had a thin algal fuzz, and calcareous red algae. Vine (1974) and Brock (1979) reported similar results. Different exposure times, depths, and techniques complicate comparisons among studies. However when values are standardized for days of exposure, my results compare well with others (Table 2). Birkeland's results from substrates exposed for 133 days are high, because they include coral recruits. His 77-day exposure gave more consistent results; those tiles averaged only one small coral recruit apiece, and algae dominated (Birkeland, 1977).

Analysis of variance revealed significant differences among study areas for both caged ($F(3,212) = 5.6$, $P < 0.001$), and exposed tiles ($F(3,232) = 17.8$, $P < 0.001$). Duncan's multiple range tests showed that caged tiles at sites M and B had similar biomasses, significantly more than site A tiles. Site P had less biomass on caged tiles than site B. On exposed tiles site M had more biomass than all the other sites. Site M lay inshore and was subject to

Figure 4. Biomass (gm per 100 cm²) of organic matter growing on porcelain tiles at each study site over a 21 day period. Values are averages for all months of HCl treated samples ± 95% confidence interval.

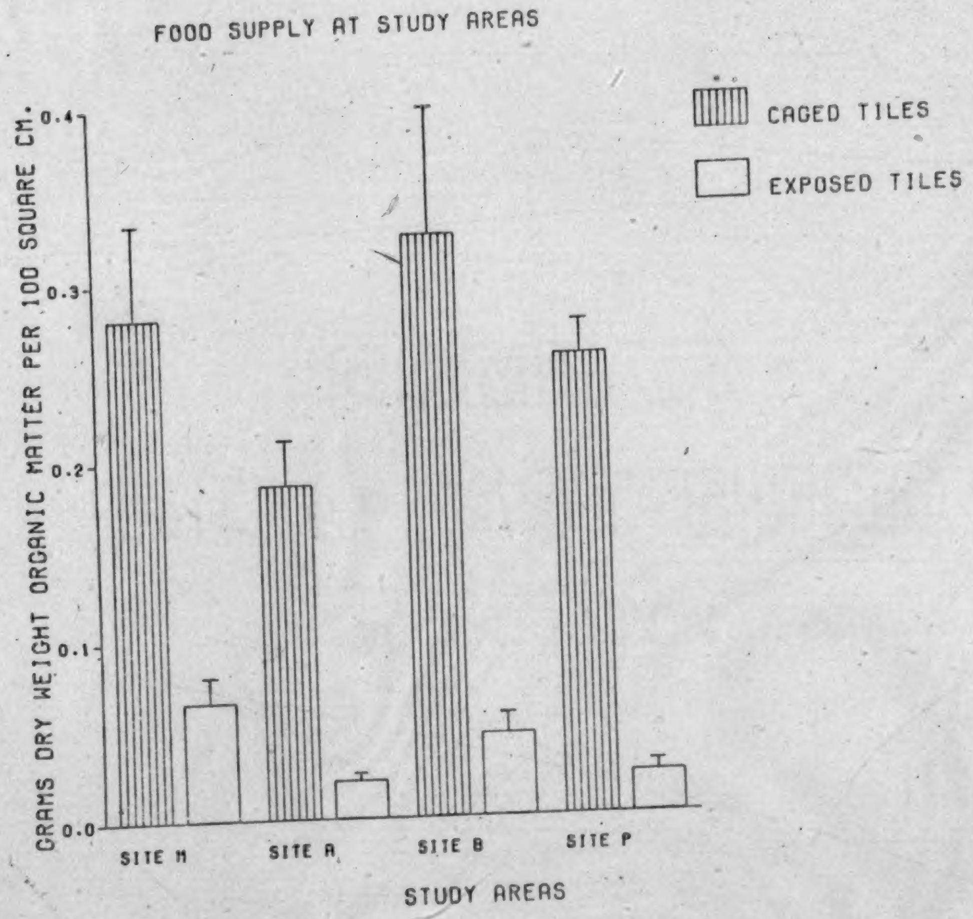

Table 2. Biomass of organic matter, primarily algae, growing on substrates in coral reef areas. Values are grams per m^2 per day.

Biomass(gm/m²/day) Caged	Exposed	Depth m	Exposure days	Location	Source
2.3 - 2.5	ND	5	17	Eniwetok	1
2.7	0.2	13	30	Red Sea	2
ND	0.3 - 0.4	9	77	Panama	3
1.4 - 1.8	0.6 - 1.3	ND	133	Panama	3
2.0	ND	2	64	Guam	4
1.0 - 1.9	0.1 - 0.4	13	21	Barbados	5

References:

1: Bakus, 1967
2: Vine, 1974
3: Birkeland, 1977
4: Lassuy, 1980, and pers. comm.
5: present study

terrestrial runoff, particularly during heavy rains. Site A lay further offshore, in deeper water where lowered light levels probably resulted in smaller algal standing crops (Vine, 1974). The dense coral and gorgonian cover at site P shaded the bottom, with lowered potential food supply as a result.

Extrapolating from these results to actual food supply at each study area is difficult. The assumption that algae settle and grow on porcelain tiles and coral surfaces in the same way has not been tested. Researchers generally look at either artificial substrates (Vine, 1974; Birkeland, 1977; Brock, 1979; Montgomery, 1980a, 1980b), or natural ones (Stephenson and Searles, 1960; Earle, 1972; John and Pople, 1973; Conner and Adey, 1976; Brawley and Adey, 1977; Lassuy, 1980; Lobel, 1980; Montgomery, 1980a, 1980b), but not both. Vertically placed plastic panels and limestone surfaces did not support identical algal flora in Australia (Day, 1977).

Assuming that tiles approximate true coral, the actual surface area of algae at each study area is unknown for reasons presented in the previous section. Moreover, coral surfaces are but one of several substrates grazed by parrotfish (see Chapter 7). The amount and type of algae growing on sand or sponges was not studied, nor were the algal mats of damselfish. Brawley and Adey (1977) presented biomass estimates for damselfish territories as wet, rather than dry weights, making comparisons with other studies difficult. It is clear, however, that damselfish algal mats form a rich, if restricted food source (Robertson et al., 1976; Lassuy, 1980; Lobel, 1980). The overall substrate heterogeneity, and the existence of numerous damselfish meant that food was probably patchily distributed at site M, and to a lesser extent at site A. The homogeneous coral cover at the barrier reef sites, B and P, likely resulted in more evenly distributed food.

I did not investigate algal species composition, or chemical constituents, both of which would affect food quality. Hawkins (1981) found that the sea urchin, *Diadema antillarum*, grew best on encrusting coralline algae, which surpassed both filamentous epipelic and endolithic algae in organic content. On the other hand, Montgomery and Gerking (1980) showed that two Gulf of California damselfish preferred red and green algae to brown and calcareous algae, all of which differed in ash, calorie, carbohydrate, lipid and protein content. While differences among study sites in food quality were possible, they seemed unlikely since algal samples from different sites appeared similar.

The detailed feeding ecology of parrotfish would be a complete study in itself. My results form a preliminary attempt to quantify parrotfish food abundance, and they allow me to rank study areas in terms of food abundance. Site M, lying inshore, had the greatest food supply and grazing substrate. Site B, lying offshore in clear, unshaded water, had a moderate food supply, although slightly less dead coral than the other sites. Site A, in deeper water, and site P, with shading from dense corals and gorgonians, had the least available food. Any differences in parrotfish behaviour related to food supply would be expected to mirror these differences among study sites.

C. Competitors

The densities of herbivores, planktivores, piscivores and other fish at each study site are given in Table 3. Feeding categories are taken from Randall (1967) and Hobson (1968, 1974). Parrotfish densities were excluded since their numbers were estimated in a slightly different fashion. Values for sites M, B and P are the averages of two surveys.

Site A, surveyed once, had the fewest species but the most individuals. The two barrier reef sites, B and P, had the most species per unit area, but the fewest individuals; site M had as many species as sites B and P, but was twice their size. At most, only 45 species (parrotfish excluded) were seen on these surveys. No doubt more were present. Smith and Tyler (1975) counted 47-53 species on a small patch reef in the Virgin Islands. They included many small cryptic species which I ignored, and which, with the exception of cleaning gobies (*Gobiosoma* spp.), rarely interact with parrotfish.

Eupomacentrus planifrons made up 94% of the herbivorous damselfish at site M, 99% at site A, 79% at site B, and 70% at site P. Its densities were high at the two sites, M and A, with staghorn coral, and were much lower offshore at

Table 3. Density of fish (parrotfish excluded) and total number of species counted during surveys at study sites. Densities are given as fish per 1000 m².

	Site M	Site A	Site B	Site P
Herbivores:				
Damselfish[1]	540	600	53	47
Surgeonfish[2]	4	1	27	41
Planktivores[3]:	997	1206	1138	1114
Piscivores[4]:	32	19	24	35
Others[5]:	134	63	195	164
Total individuals[6]:	1707	1889	1437	1401
Total species[6]:	44	25	42	43

Species in order of abundance:

[1] *Eupomacentrus planifrons*, *Microspathodon chrysurus*, *E. variabilis*, *E. diencaus*

[2] *Acanthurus bahianus*, *A. chirurgus*, *A. coeruleus*

[3] *Chromis cyanea* (*C. multilineata* was too abundant to be counted), *E. partitus*, *Clepticus parrae*, *Inermia vittata*

[4] *Cephalopholis fulva*, *Petrometopon cruentatum*, *Epinephelus adscensionis*, *E. guttatus*, *Aulostomus maculatus*, *Rypticus saponaceus*, *Serranus tabacarius*, and various scombrids, synodontids, lutjanids and muraenids

[5] labrids, chaetodontids, *Hypoplectrus* spp., *Serranus tigrinus*, mullids, pomadasyids, *Canthigaster rostrata*, monacanthids, ostracionids, and other families

[6] Parrotfish excluded

sites B and P. Surgeonfish (mostly *Acanthurus bahianus*), the other major herbivores, were most numerous at sites B and P, but did not reach great densities anywhere. Planktivores, the most abundant individuals, were most common offshore. Piscivores, primarily small serranids, could not be reliably counted because of their secretive habits, but appeared to be most numerous at site P, which had the densest coral cover (Table 1).

The impact of planktivores, piscivores and other species on adult parrotfish social behaviour is probably much lower than that of herbivorous damselfish. Parrotfish interacted regularly with damselfish (see Chapter 7), but only rarely with the other groups. Planktivores could indirectly affect scarids by consuming their eggs (Rose, 1972; Colin, 1978), and suppressing their spawning activity. This latter does not appear to happen; both planktivores and spawning are most common on offshore reefs (Goldman and Talbot, 1976; Gladfelter and Gladfelter, 1978; Johannes, 1978; Johnson and Gladfelter, 1980). Predation, while a significant force in reef fish evolution, is less important as a proximate determinant of social behaviour in parrotfish. Authors who stress its importance generally deal with small species which, unlike adult parrotfish, are closely tied to shelter (Sale, 1980). Crepuscular and nocturnal predation probably strongly affect parrotfish cover-seeking and migratory behaviours at twilight (Hobson, 1965, 1972, 1973; Ogden and Buckman, 1973; Dubin and Baker, 1981), but I saw predation during the daytime only rarely, and then only on juveniles. Others (Randall and Randall, 1963; Colin, 1978) have seen predation interrupt group spawning in parrotfish. However, the appearance of a predator on the reef results in only a short-term behavioural change such as moving towards cover (Buckman and Ogden, 1973; pers. obs.). Moreover, piscivores in Barbados were not large; the moray eel *Gymnothorax moringa*, was the largest (SL 1 m). Parrotfish over 120 to 150 mm SL may be relatively free of predation during the day, provided they behave "normally" (Hobson, 1968). Their planktonic larval stage ensures that parrotfish at all study sites shared the same gene pool (Fricke, 1975a). Like many reef species, they probably possessed equivalent anti-predator adaptations such as schooling when small, constant vigilance, and avoidance of, or even defensive responses towards predators (Eibl-Eibesfeldt, 1962; Fricke, 1975b; Coates, 1980a, 1980b; Dubin, 1982), and rapid growth rates (Randall, 1961b), allowing them to outgrow their predators.

Thus the most striking difference between study areas was the density of the territorial, herbivorous damselfish, *Eupomacentrus planifrons*. This species might affect parrotfish social behaviour by excluding them from parts of the reef, interfering with their feeding, forcing them to form massive schools to feed successfully, or ultimately disrupting their social groupings (Barlow, 1974; Alevizon, 1976; Robertson et al., 1976; Kaufman 1977). A comparison of parrotfish behaviours at sites A and M with sites B and P would reveal such effects.

D. Abiotic variables

Of the almost infinite array of abiotic variables that might affect parrotfish behaviour - tides, temperature, light levels- few differed even slightly among study sites. However, those factors influencing spawning site suitability, namely prevailing currents, distance from shore, and proximity to promontories, did vary among my sites.

Currents were encountered 146 times during 514 dives in 1978-9 (Table 4). They were not independent of month in their occurrence ($X^2(11) = 26.4$, $P < 0.01$), being most frequent from March through October, and particularly common in May-June and September-October. Data from 1976-7 were not continuous but showed similar trends. The period of increased currents was the same as, or soon after, the spawning peak for Caribbean fish (Munro et al., 1973; Colin, 1978), when juvenile recruitment is at its highest (Powles, 1975; Luckhurst and Luckhurst, 1977; Chapter 4, this study).

Pairwise contingency chi-square analysis showed that current strength, direction, and presence or absence were independent of tides, or moon phase,[1] so currents were not

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[1] Current strength and moon phase, $X^2(3) = 6.5$, ns; current strength and tides, $X^2(3) = 0.92$, ns; current direction and moon phase, $X^2(3) = 5.8$, ns; current direction and tides, $X^2(3) = 2.2$, ns; current presence and moon phase, $X^2(3) = 1.3$, ns; current presence and tides, $X^2(3) = 1.1$, ns.

Table 4. Number and percent of dives during 1978-9 in which currents were encountered.

	With current	No current	% with current
1978:			
May	12	23	34
June	11	18	38
July	5	16	24
August	7	14	33
September	17	32	53
October	8	13	38
November	4	15	21
December	6	33	15
1979:			
January	3	39	7
February	6	33	15
March	16	34	32
April	9	24	27
May	26	32	45
June	16	42	28

primarily tidal in origin. Emery (1972) reported that tides added a slight east-west component to the primarily north-south current vector. I found that only 7.5 % of all currents flowed in an east-west direction. Emery (1972) suggested that the currents were part of gyres formed in the wake of Barbados. Current meters placed 1 km offshore in his study showed that current direction often switched 180° within a few days. He attributed these shifts to oscillations between a pair of gyres.

Currents were far more common at sites A, B and P than inshore at site M. I encountered them in 34 % of the dives at the offshore sites, but in only 14 % inshore ($X^2(1) = 20.3$, $P < 0.001$). Site M was more stagnant, and was well separated from offshore waters by intervening reefs. Salps and siphonophores, indicators of oceanic waters (Gladfelter et al., 1980), were often encountered at the offshore sites. Thus sites A, B and P, were closer to oceanic waters, and more often swept by currents which would remove eggs from the reef.

No sites contained large promontories or coral heads exceeding 1 to 2 m in height. However, sites A and P lay less than 20 m from reef slopes extending to depths below 30 m. Site M also had a short slope reaching 18 m at its seaward end.

Thus differences among sites in suitability for broadcasting eggs were marked. Site M was probably a poor area for spawning because of its inshore position and relatively stagnant water. All the other sites were exposed to currents, close to offshore waters, and near reef slopes, although site B lay further from a reef slope than sites P and A.

E. Summary and discussion

Each site showed some different combination of ecological factors which might affect parrotfish behaviour. Site M was covered mainly by branching corals and rubble, had a good, patchily distributed food supply but dense populations of damselfish competitors, and was a poor spawning site. Site A had branching corals, a low, somewhat patchy food supply, dense populations of damselfish, and was a good spawning site. Site B had scattered coral heads, a moderate, evenly distributed food supply, few damselfish, and was a good spawning site. Site P had dense coral heads, a low, even food supply, few damselfish, and was a good spawning site.

Hypotheses concerning effects of ecological variables on social systems can now be stated.

1. If cover affects parrotfish behaviour, then site M and site A parrotfish should show more behavioural similarities with each other than with those at sites B and P.
2. If damselfish affect parrotfish social systems by excluding them from parts of the reef, their numbers should inversely correlate with those of parrotfish.

This effect should be most visible at site M where damselfish densities are high and heterogeneity is great.

3. If damselfish disrupt parrotfish feeding, then feeding rates at sites M and A should be lower than those at sites B and P. Feeding rates should also be more variable in dense damselfish areas if fish compensate for interrupted feeding within damselfish territories by more intensive feeding when outside them.
4. If food is a defended resource then food abundance should determine the quality of space, and high quality areas should be most heavily sought after (Krebs, 1971; Ewald and Carpenter, 1978; Myers et al., 1979; Vines, 1979; Ewald et al., 1980). Thus competition for space in terms of intruder pressure should be greatest at site M where food is most abundant, and lowest at sites A and P where it is most scarce (Davies, 1978). Likewise territories should be smallest at site M under this assumption (Slaney and Northcote, 1974; Simon, 1975; Dill, 1978; Kodric-Brown and Brown, 1978; Ebersole, 1980; Hixon, 1980b; Larson, 1980c).
5. On the other hand, if space for spawning is an important defended resource, then site M should be the least desirable, and sites A, B and P, the most.

Each of these hypotheses is treated more fully in the following chapters and subsequent discussion.

IV. Parrotfish populations: composition, fluctuations and recruitment

Information from weekly grid surveys allowed me to assess parrotfish species composition and population structure at each study area. Besides providing baseline data on parrotfish densities, this knowledge allowed determination of what factors controlled population size (e.g. food supply, territoriality) at each site. Parrotfish often move freely over long distances, between different feeding areas, to and from night-time sleeping spots, or day-time spawning locations (Winn et al., 1964; Bakus, 1967; Randall and Randall. 1963; Hobson, 1972, 1973; Ogden and Buckman, 1973; Barlow, 1975; Choat and Robertson, 1975; Colin, 1978; Dubin and Baker, 1981). An analysis of fluctuations in their numbers in relation to tides, currents, and time of day allowed me to test whether such migrations occurred, and to pinpoint their functions. Seasonal cycles in both juvenile and adult numbers were also investigated, as it was important to determine the stability of populations. Data included the total number of each parrotfish species and phase (juvenile, Iph, Tph), along with the time, currents, tidal state, moon phase, and temperature.

A. Composition and density

The densities of parrotfish at each study area, averaged over all grid surveys, are given in Table 5. Five species: *Sc. iserti* (Bloch), *Sc. taeniopterus* Demarest, *Sc. vetula* (Bloch and Schneider), *Sp. aurofrenatum* (Cuv. and Val.), and *Sp. viride* (Bonnaterre), were common on Barbados' west coast (Plates 2 to 6). Two others, *Sp. atomarium* (Poey), and *Sp. rubripinne* (Cuv. and Val.), were seen infrequently, and a third, *Sp. chrysopterum* (Bloch and Schneider), although seen on rare occasions, was never counted during grid surveys.

Comparisons between 1976-7 and 1978-9

The species composition at sites M and B from the two study periods, 1976-7 and 1978-9, agreed well. However, the numbers of Iph *Scarus* spp. were greater in 1978-9 (Mann-Whitney U Test, site M: $z = -7.0$, $P < 0.001$, site B: $z = -4.6$, $P < 0.001$).[2] Iph *Sp. aurofrenatum* were also more numerous in 1978-9 (site M: $z = -5.2$, $P < 0.001$; site B: $z = -2.2$, $P < 0.05$), as were juvenile *Scarus* and *Sp. aurofrenatum* at site M ($z = -2.9$, $P < 0.01$; $z = -3.1$, $P < 0.01$ respectively).

The numbers of Tph fish did not increase significantly between years, which suggests that the change was not attributable to observer bias. It could be argued that 1976-7 surveys gave lower densities because, being less

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[2] The increase was due primarily to *Sc. iserti*. *Sc. vetula* increased slightly. *Sc. taeniopterus* did not at site M, but did at site B.

Table 5. Average density of parrotfish per 1000 m² at each study area in 1976-7 and 1978-9, calculated from grid surveys, the number of which is shown in parentheses.

	Site M		Site A	Site B		Site P
	1976-7 (58)	1978-9 (50)	1978-9 (4)	1976-7 (22)	1978-9 (49)	1978-9 (48)
Juveniles:						
Scarus:	23.4	37.7	10.8	0.3	0.4	1.7
Sp. aurofrenatum:	2.3	3.2	8.0	1.9	1.3	2.6
Sp. viride:	4.5	4.6	2.3	0.03	0.03	0.1
Total juveniles:	30.2	45.5	21.2	2.2	1.7	4.4
Adults:						
Sc. iserti:						
Iph	44.6	70.1	9.0	27.1	42.5	59.9
Tph	1.9	1.0	2.5	7.4	7.8	9.4
Sc. taeniopterus:						
Iph	14.9	14.8	28.3	15.7	20.3	9.3
Tph	1.2	1.6	4.2	2.2	2.0	1.7
Sc. vetula:						
Iph	9.1	12.2	2.3	0.2	0.7	1.1
Tph	1.2	1.8	0.3	0.03	0.1	0.4
Sp. aurofrenatum:						
Iph	5.1	8.2	10.7	8.8	10.5	14.7
Tph	1.0	1.9	3.7	3.7	3.5	5.2
Sp. viride:						
Iph	13.4	15.7	6.8	1.1	1.3	5.0
Tph	1.0	0.9	0.3	0.0	0.02	0.7
Sp. atomarium:	0.3	0.6	0.0	0.0	0.0	0.0
Sp. rubripinne:	0.0	0.0	0.0	0.2	0.05	0.01
Total adults[1]:	95.6	130.4	68.2	66.4	88.8	107.5

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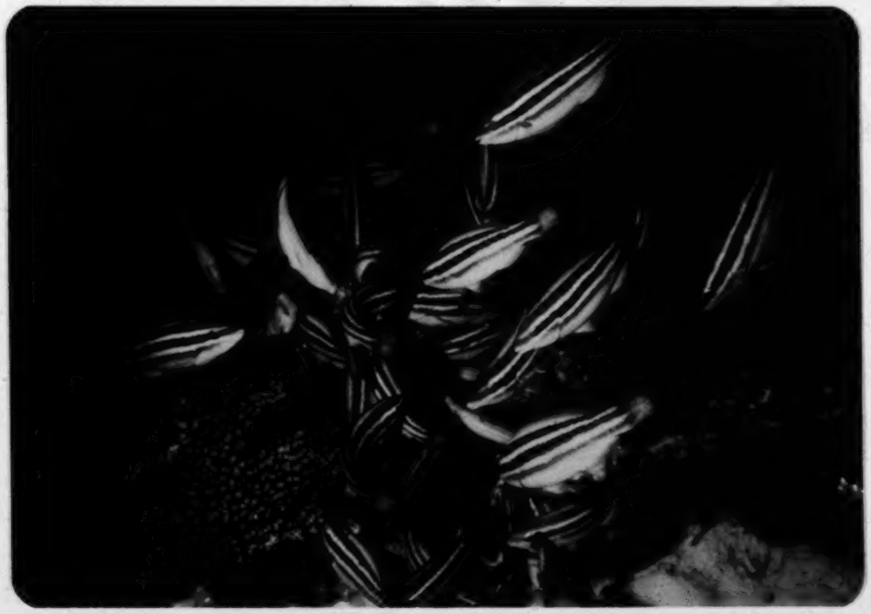
[1] Includes some unidentified *Scarus* spp. seen in the early morning.

Plate 2. A Tph *Sc. iserti* (right) chases an Iph conspecific.

Plate 3. Iph and Tph *Sc. taeniopterus*. The Iph *Sc. taeniopterus* (above) are part of a large feeding aggregation in the vicinity of site A.



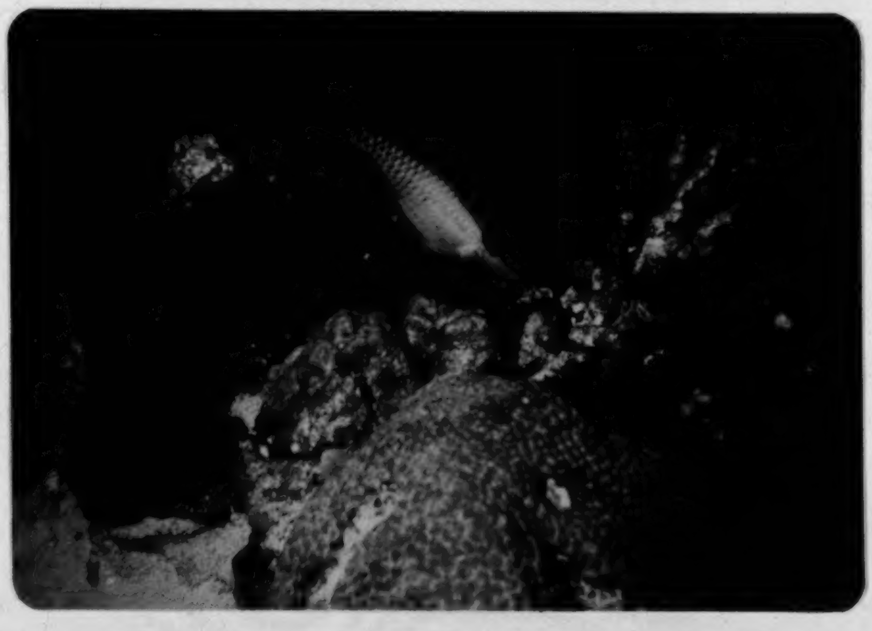


Plate 4. Iph and Tph *Sc. vetula*. An Iph *Sp. aurofrenatum* is visible in the lower right corner of the upper photograph.

Plate 5. Iph and Tph *Sp. aurofrenatum*. The Tph *Sp. aurofrenatum* is holding an aggressive tailstand position (Chapter 7). One Iph *Sp. aurofrenatum* arches submissively in front of the Tph male.

Plate 6. Iph and Tph *Sp. viride*. The Tph male (below) is being cleaned by two *Gobiosoma* spp.

Warner, 1978).

Massive feeding aggregations consisting of 10 to 30 Iph *Sp. viride*, 50 to 75 Iph, and 1 to 3 Tph *Sc. taeniopterus*, 2 to 10 Tph *Sc. iserti* and 20 to 100 *Acanthurus bahianus* regularly passed through site A (Plate 3). None were encountered at site A during grid surveys. The major species seen there were *Sp. aurofrenatum*, and *Sc. taeniopterus*, which was more common at site A than anywhere else.

The common barrier reef species were *Sc. iserti*, *Sc. taeniopterus*, and *Sp. aurofrenatum*. At site B, *Sp. aurofrenatum*, and Iph *Sc. iserti* were less common than at site P, while *Sc. taeniopterus* was more abundant. *Sc. vetula* and *Sp. viride* were rarely seen at these two sites, although they were encountered more often at site P than at site B. The *Sp. viride* seen at sites B and P were generally solitary. Likewise the few *Sc. vetula* encountered offshore appeared to be stragglers or migrants rather than residents. *Sp. rubripinne* occasionally appeared offshore, apparently engaged in courting activities; Tph males moved with small groups of Iph fish, and interacted aggressively with other males.

The age structure of parrotfish populations also differed among study sites. Juvenile *Scarus* and *Sp. viride* were abundant at site M, common at site A, and virtually absent from sites B and P. Juvenile *Sp. aurofrenatum*, on the other hand, were most abundant at site A, and were regularly encountered at all sites. These differences suggest that juveniles may be settling selectively in certain parts of the reef, particularly inshore areas, and that *Sp. aurofrenatum* juveniles settle in a broader range of habitats than the other species.

Tph males of *Sc. iserti*, *Sc. taeniopterus* and *Sp. aurofrenatum* were less abundant inshore at site M than elsewhere, both in absolute terms (Table 5), and relative to numbers of Iph fish (Table 6).

Site M could thus be categorized as primary nursery habitat, with a diverse assemblage of mostly Iph parrotfish. The other sites harboured fewer juveniles, but more Tph males for the three most widespread species, *Sc. iserti*, *Sc. taeniopterus* and *Sp. aurofrenatum*. Each site held a different balance of these species, with *Sp. aurofrenatum* spread most evenly throughout. Site A had the fewest *Sc. iserti*, and the most *Sc. taeniopterus*. The reverse was true for site P. It was primarily because of their broad distribution that I chose these three species for detailed behavioural studies.

The differences among study areas in a species' density cannot be explained by one single factor. Exclusion by damselfish may have accounted for the lack of *Sc. iserti* during the day at site A, although large numbers passed through it at sunrise and sunset (Dubin and Baker, 1981). *Sc. vetula* and *Sp. viride* dwelt primarily inshore, *Sc. vetula* was closely tied to staghorn coral, and both species were more shallowly distributed than the others (Robertson

Table 6. Average number of Iph parrotfish per Tph-male at each study area, calculated from grid surveys.

	Site M		Site A	Site B		Site P
	1976-7 (58)	1978-9 (50)	1978-9 (4)	1976-7 (22)	1978-9 (49)	1978-9 (48)
Sc. iserti:	23.0	70.0	3.6	3.7	5.5	6.4
Sc. taeniopterus:	12.4	9.3	6.7	7.1	10.0	5.5
Sc. vetula:	7.6	6.8	7.7	6.7	7.0	2.8
Sp. aurofrenatum:	5.1	4.3	2.9	2.4	3.0	2.8
Sp. viride:	13.4	17.4	22.7	ND	66.0	7.1

and Warner, 1978; next chapter).

There was no clear relation between an area's food supply and total adult densities (Figure 4 and Table 5). Site M had the largest biomass of food and the greatest parrotfish density. However site P had a much lower food supply, even considering its greater amount of dead coral grazing substrate (Table 1), yet the second most dense parrotfish population. Choat and Robertson (1975) reported a similar poor relation between grazing surface and parrotfish density. Luckhurst and Luckhurst (1978b) and Leum and Choat (1980) found a correlation between substrate rugosity (an index of actual surface area taken by moulding a chain to the bottom contours, and computing the ratio of this length to the linear distance) and the number of individual fish. Site P's greater substrate rugosity due to its dense coral cover may have accounted for its abundant parrotfish populations. A more detailed analysis of each species' relationship to various substrate variables is presented in the next chapter.

Comparisons with other studies

The total densities of parrotfish measured here accord well with other studies. I counted 89 to 126 scarids (adults and juveniles combined) per 1000 m² (Table 5). Frydl and Stearn's (1978) estimates for site B in Barbados (their Bank Reef site), made in 1975-6 accord well with mine for 1976-7. Theirs for a portion of site M (their Moorings site) are lower, because their transect covered only one section of this heterogenous site where numerous damselfish excluded Iph parrotfish (see next chapter). Randall (1963a) estimated 67 to 121 parrotfish per 1000 m^2 from poison stations in the Virgin Islands, while Bardach (1959) got a density of 70 fish per 1000 m^2 in visual surveys at Bermuda, and Gygi (1975) estimated *Sp. viride* densities at 15.1 per 1000 m^2, in close agreement with my values at site M. Barlow (1975) counted 96 to 140 parrotfish per 1000 m^2 in Puerto Rico. Two studies from the Great Barrier Reef quote values within the range of this study; Bradbury and Goedin (1977) measured 86 fish per 1000 m^2, and Choat and Robertson (1975) estimated 45 to 425 fish per 1000 m^2. Only the values of Brock (1979) from Hawaii are high; he measured 1100 fish per 1000 m^2, but these were mostly small juveniles.

Parrotfish are as important a component of Barbadian reefs as they are elsewhere (Bardach, 1959; Randall, 1963a; Bakus, 1967; Itzkowitz, 1974; Goldman and Talbot, 1976). They made up 9.3 % of the individuals at site M, 4.5 % at site A, 5.9 % at site B, and 7.4 % at site P (Tables 3 and 5). These numbers agree well with those of Alevizon and Brooks (1975) who estimated that parrotfish comprised 8 % to 13 % of the total fish at two widely separated Caribbean locations. On a weight basis their contribution may be even greater, since scarids are generally heavier than the numerous small damselfish that made up the bulk of the individuals counted.

B. Effect of abiotic variables: tides, time, currents, weather and moon phase

Parrotfish are known to make extensive movements within and between reefs, often on a daily basis. In many geographic locations they migrate regularly between night-time sleeping spots and daytime areas (Winn and Bardach, 1960; Winn et al., 1964; Ogden and Buckman, 1973; Hobson, 1972, 1973; Collette and Talbot, 1972). Elsewhere (Dubin and Baker, 1981), I have discussed what factors determine parrotfish diurnal migrations and choice of sleeping spots. *Sp. aurofrenatum* did not migrate at dusk and dawn, while the other species did so regularly. These migrations allowed fish to exploit areas during the day that possessed unsuitable cover for sleeping spots. However, crepuscular movements occurred outside the time span of these grid surveys.

Tidal migration cycles have also been described. Bakus (1967) noted that large parrotfish moved inshore to feed at high tide. Choat and Robertson (1975) found that while the Great Barrier Reef species, *Sc. fasciatus*, moved onto the reef flat to feed at high tide, other species spawned at high or ebb tide on the reef crest or front. Spawning migrations may be linked to the time of day. Randall and Randall (1963), Barlow (1975), and Colin (1978) found that numbers of parrotfish increased over the day at spawning locations.

The same data from the comparisons among study areas were subjected to analyses of variance for differences due to tidal, diurnal or other influences. Very few tests gave significant results. Given the large number of tests performed, a certain number of erroneous significant values were expected. Thus, at sites M and B, only those trends that were consistent in both 1976-7 and 1978-9 were accepted as valid.

No trends general to all sites or species were apparent although tide-related movements seemed possible for some species at some sites. More Tph *Sc. taeniopterus* were seen offshore at low tide than at high tide (Site B, $F(2,68) = 3.4$, $P = 0.04$; Site P, $F(2,45) = 3.2$, $P = 0.05$). Iph *Sc. vetula* were also most common at site B during low tide ($F(2,68) = 4.1$, $P = 0.02$). Iph *Sc. taeniopterus* were most common at site P during flow and slack tides ($F(2,45) = 9.2$, $P = 0.0004$), and large Iph *Sp. viride* were seen there most at slack tide ($F(2,45) = 5.3$, $P = 0.009$). *Sp. rubripinne* appeared at site B only during flowing tide. I have too few observations to relate any of these movements to spawning with the exception of *Sp. rubripinne*, noted above. *Sc. taeniopterus* appears to spawn at ebb tide (Dubin, 1981).

Only a few species showed any significant diurnal trends within the time span of the study. Tph *Sp. viride* were most common at site M during the mid-morning (three to five hours after sunrise, $F(3,104) = 4.7$, $P = 0.004$). Tph *Sp. aurofrenatum* were most common at site M in the early morning (one to two hours after sunrise, $F(3,104) = 2.8$, $P =$

0.04). *Sp. viride* probably ranges widely, and may exploit different parts of the reef over the day. Tph *Sp. aurofrenatum* fed most in the early morning at site M (page 224), and as a result may have been more sedentary, and thus more often seen.

Currents had few effects on parrotfish numbers. Tph *Sp. viride* were seen least often at site M during north-flowing currents (F(2,105) = 3.7, P = 0.027). Tph *Sc. vetula* and Iph *Sp. viride* were seen most often at site B when currents flowed offshore (F(3,67) = 4.4, P = 0.007; F(3,67) = 4.9, P = 0.004). Juvenile *Scarus* were seen most at site P during south-flowing currents (F(2,45) = 5.3, P = 0.009). Again, these patterns may have related (with the exception of juvenile scarids) to spawning migrations, or to individuals becoming lost because of unusual water conditions. More Iph *Sc. vetula* were seen at site B on overcast days (F(1,34) = 5.2, P = 0.03), and it has been shown that homing parrotfish become disoriented under cloudy conditions (Winn et al., 1964).

More parrotfish were counted at site M in both years on calm days than on days with heavy chop or swells (F(1,106) = 17.9, P = 0.0001). This was partly an artifact of observer bias, as surveys were more difficult to complete when the water was disturbed. Also, parrotfish tended to remain closer to cover on such days, and so may have been overlooked.

No trends in numbers of fish related to moon phase were detected.

Abiotic variables could affect the numbers counted during a grid survey in several ways. They could cause real changes in fish numbers by stimulating migrations into or out of study areas. Alternatively, abiotic variables could cause fish to behave in a more conspicuous fashion, e.g. swim in more open areas, and so improve the chances that I would count them. This could explain differences in sightings of juvenile *Scarus* at site P during south-flowing currents, or of total parrotfish at site M on days with substantial wave activity. However, parrotfish were generally conspicuous and would be overlooked only if they hid under cover, something which they did rarely (see Chapter 7). Finally, a fish's swimming speed, vagility, or pattern of movements through its home range could have changed under certain abiotic conditions so that I was not counting different fish, but merely recounting the same ones more or less often. This explanation seems unlikely. The home ranges of the Iph fish, which made up the bulk of my sightings, were small enough to make resightings unlikely (see Chapter 7). Also, such responses should have appeared at all sites for a given species, rather than at just a few, as was the case. My impression was that swimming speed remained constant over the day, with the exception that Tph males circled their territories more rapidly when courting. However, increases in apparent numbers did not appear during each species' regular spawning time, as would be expected if more active fish were counted more often. Thus, it is unlikely that changes in movement patterns varied sufficiently in this study to account for any observed fluctuations.

In summary, populations at the study areas were stable throughout the day, and numbers changed only rarely in relation to tidal cycles, time of day, currents or weather conditions. Most of the fluctuations concerned species that were migrants or stragglers (*Sc. vetula*, *Sp. viride*, *Sp. rubripinne* at sites B and P) which may have been disoriented, or were responding to currents or tidal conditions favourable for spawning. With few exceptions, resident populations were constant despite varying abiotic conditions.

C. Seasonal trends in juvenile recruitment and adult populations

The grid surveys from 1978-9 at sites M, B and P spanned 14 months continuously, and were suitable for analysis of seasonal trends. Since the 1976-7 data were not continuous, they were excluded from this analysis. Site A, surveyed only four times, was also excluded. I used the computer package SPSS - Regression to investigate trends in numbers over time in weeks from the beginning of the study by fitting the curve:

$$\text{No. fish} = a + b(\text{weeks}) + c(\text{weeks})^2 + d(\text{weeks})^3 + \ldots,$$

where a to d are constants.

The cyclic nature of juvenile populations was further tested by fitting a periodic (sine) curve to the total number of juveniles at site M (BMDP3R - Nonlinear Regression). Finally Pearson's correlation coefficients were calculated between numbers and water temperatures.

Fitting a polynomial equation to a set of points is useful when nonlinear trends are suspected, but the exact model is unknown (Draper and Smith, 1966; Snedecor and Cochrane , 1980). The polynomial equation with the lowest order that leaves no significant unexplained variation in the data is chosen as the best fit. The order of a polynomial is always one greater than the maximum possible number of critical points (inflection points or local minima and maxima) in the curve (Herstein, 1975). Knowledge of the number of critical points is necessary to detect the period of any cycles in the curve. Inspection of Figure 5 showed that two critical points (one minimum and one maximum) were present. Therefore third-order equations were suspected to give the best fit, but polynomials up to an order of six were fitted to the square-root transformed data to check for higher-order cycles.

Juvenile recruitment

There were clear seasonal cycles in juvenile numbers (Figures 6 and 7, Table 7), with year-round recruitment, particularly at site M where juveniles of all species were abundant. Juvenile *Scarus* spp. were most common from June to September, *Sp. viride* from July to October. Juvenile *Sp.*

Figure 5. The number of juvenile *Scarus* spp. counted at each area over the study period. P78 refers to site P in 1978-9, B78 to site B in 1978-9, and so on.

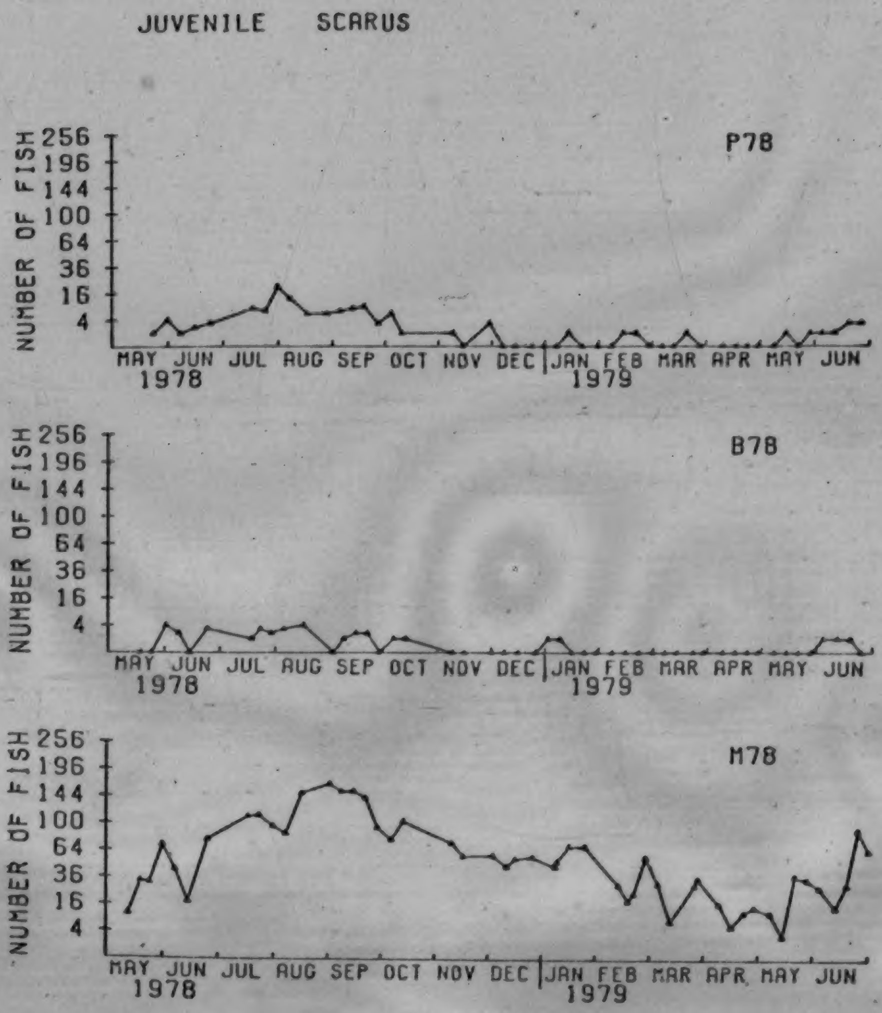
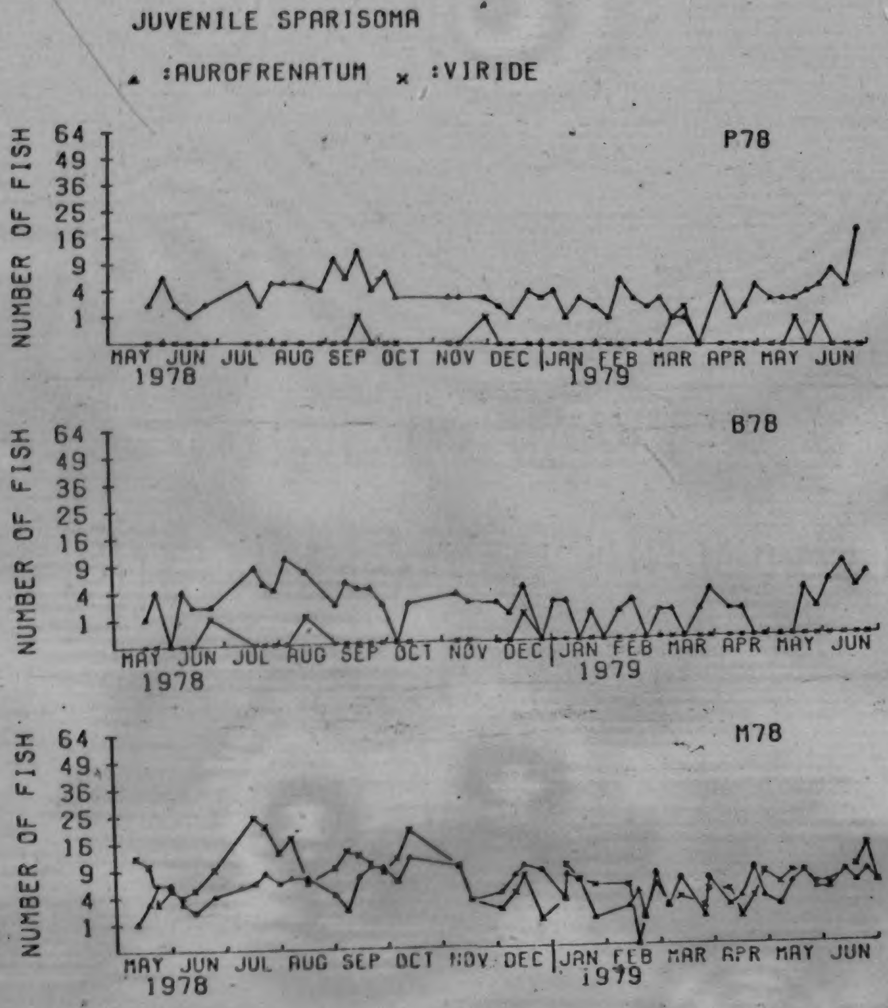


Figure 6. The number of juvenile *Sparisoma aurofrenatum* and *Sp. viride* seen at each area over the study period. Study areas as in Figure 5.



aurofrenatum were seen more evenly over the year although slight increases at all sites from July to September or October were apparent.

At all study areas where juveniles were encountered, third-order polynomials gave the best fit (Table 7). This meant that, as expected, there were two critical points, i.e. one complete cycle, over the 14 month study. Luckhurst (1977) found three critical points, i.e. 1.5 cycles, in his 18-month study.

The cyclic nature of juvenile populations was underlined when a sine curve was fitted to the total number of juveniles seen at site M over 1978-9 (Figure 7). The curve:

$$Y = 78.4 - 60.2 \left(\mathrm{Sin}\ 0.115(\mathrm{Weeks} - 141) \right)$$

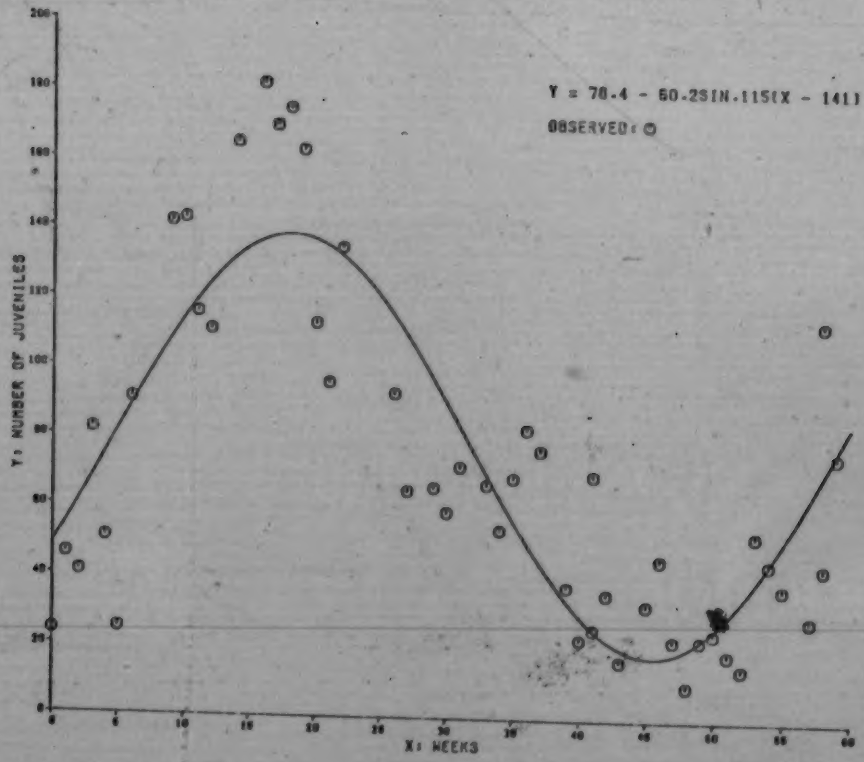
showed a maximum about 16 weeks after the start of the study, i.e. in September 1978.

The juvenile numbers included fish up to 50 or 60 mm in length which may have been recruited some months before the September peak. I saw new recruits (from 8 to 15 mm in total length), throughout the year at site M with marked peaks in late May, 1978 and late June, 1979 (Figure 8). At sites B and P the new recruits (*Sp. aurofrenatum* only) appeared from late March to June. Powles (1975) analysed ichthyoplankton caught off Barbados' west coast in 1972 and 1973. He observed large numbers of scarids in December, January, March, April, August and October, and concluded that there were two yearly peaks in larval abundance, one from March to

Table 7. Summary of polynomial regression of fish number (square root transformed) on weeks since the start of the study in 1978. The order of significant polynomial terms is indicated as is the value of r^2 for the third-order regression in parentheses. An order of 1 indicates that only a linear relation between number and weeks was significant. An order of 1,3 means that both the terms *weeks* and *weeks*^{3} added significantly to the regression. ND indicates that too few fish were present to be analysed. Blank spaces appear where there were no significant regressions.

	Site M n = 50	Site B n = 49	Site P n = 48
Juveniles:			
Scarus spp.	1,2,3 (0.76)	1,3 (0.45)	1,3 (0.67)
Sp. aurofrenatum	3 (0.25)	1,3 (0.45)	3 (0.44)
Sp. viride	1,3 (0.48)	ND	ND
Total juveniles	1,2,3 (0.78)	1,2,3 (0.57)	1,2,3 (0.61)
Adults:			
Sc. iserti			
Sc. taeniopterus	2 (0.14)	1,2 (0.41)	
Sc. vetula	2,3 (0.31)		
Sp. aurofrenatum		2 (0.14)	1,2 (0.29
Sp. viride	1 (0.42)		3 (0.17)

Figure 7. Plot of total juvenile parrotfish seen at site M versus weeks from the start of the study in May 1978. The solid line is a sine curve fitted to the data by the BMDP3R nonlinear regression program.



May and one from August to October. Juvenile scarids (SL 7 to 50 mm) were most abundant in Florida seine samples during June through September, and in December, with the smallest seen in August (Springer and McErlean, 1962b). Winn and Bardach (1960) found scarids below 25 mm SL in August in Bermuda. A fall peak in new recruits is not visible in Figure 8, but year to year variations in recruitment are possible (Russell et al., 1974, 1977; Luckhurst, 1977; Talbot et al., 1978).

The duration of the pelagic stage of most reef fish larvae is a mystery. I estimated a six to eight week larval stage for scarids based on Powles' (1975) spring ichthyoplankton peak of March and April, and my recruitment peak in late May and June. This value agrees well with the 2.5 month pelagic period for the surgeonfish *Acanthurus triostegus* in Hawaii (Randall, 1961a). It is somewhat longer than the four week larval stage of the blenny, *Ophioblennius atlanticus* (M. Labelle, pers. comm.). Measurement of daily growth rings in otoliths of recently recruited fish (Brothers et al., 1976; Ralston, 1976;) will allow accurate determination of their pelagic period.

The environmental factors that control juvenile recruitment cycles are unclear. Their numbers correlated closely with water temperature at all study areas (Table 8). Luckhurst (1977) attributed a similar relation in Curacao to temperature-dependent spawning. Russell et al. (1974, 1977) also found the highest juvenile recruitment on the Great

Figure 8. Numbers of recently recruited scarids at site M, B and P in 1978-9. Recent recruits measured less than 15 mm in total length (Leis and Miller, 1976). Sc. stands for juvenile *Scarus*, Sp. a. for *Sp. aurofrenatum*, and Sp. v. for *Sp. viride*.

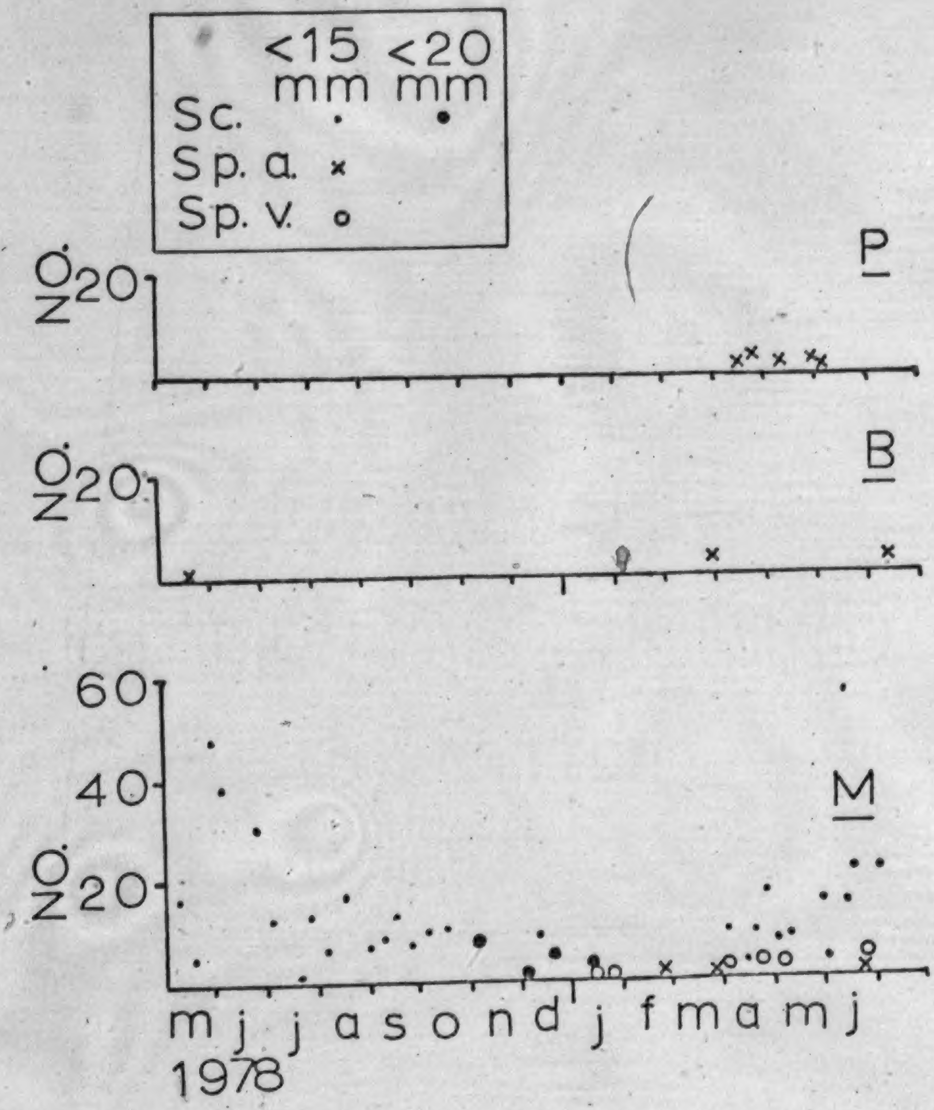


Table 8. Pearson correlations between number of fish (square-root transformed) and water temperature during each grid survey in 1978-9. The significance of the correlation is indicated by asterisks:
*: P < 0.05. **: P < 0.01. ***: P < 0.001.

	Site M n = 50	Site B n = 49	Site P n = 48
Juveniles:			
Scarus spp.	0.58 **	0.44 **	0.58 ***
Sp. aurofrenatum	0.38 **	0.48 ***	0.47 ***
Sp. viride	0.55 **	ND	ND
Total juveniles	0.62 ***	0.55 ***	0.57 ***
Adults:			
Sc. iserti	0.03 ns	0.30 *	0.20 ns
Sc. taeniopterus	-0.03 ns	-0.07 ns	0.25 *
Sc. vetula	-0.25 *	-0.21 ns	-0.31 *
Sp. aurofrenatum	0.14 ns	-0.01 ns	0.20 ns
Sp. viride	0.24 *	0.17 ns	-0.26 *

Barrier Reef during the warmer summer months, and suggested that settlement was timed to occur when primary production and food supply were increasing. The damselfish, *Pomacentrus wardi*, recruits throughout the year in the same location with a spring-summer peak, but two other pomacentrids show constant recruitment (Sale, 1979). Settlement of the temperate New Zealand wrasse, *Pseudolabrus celidotus*, occurs in the warm water months when food levels are high (Jones, 1980). Johannes (1978) concluded that spawning peaks were best related to shifts in prevailing currents that improve the chances for larvae to be returned to the reef. The recruitment peak of scarids in Barbados corresponded with the period of increased current which may represent a seasonal shift in larvae-retaining gyres (Table 4).

Few studies have been able to show that seasonal spawning cycles exist in tropical fish. Scarids in Panama and Barbados spawned year-round (Robertson and Warner, 1978; this study). Munro et al. (1973), and Thompson and Munro (1978) analysed gonadal maturity of numerous reef fish in Jamaica and concluded that peak spawning occurred at minimum water temperatures in February, March, and April. *Eupomacentrus planifrons* spawned year-round in Jamaica , with a slight peak in April (Williams, 1978). The only behavioural study to date on parrotfish spawning seasonality (Colin, 1978) contradicted these findings; *Sc. iserti* group spawned in Jamaica six times more often in June than January. Clavijo (1980a) found no evidence for seasonal cycles in the spawning of *Sp. aurofrenatum* over a three-year period in Puerto Rico. Juvenile recruitment in this species was more even over the year than in *Scarus*. Pair spawners may produce larvae that are spread evenly over the year, and seasonal peaks could be due primarily to the addition of larvae from group spawnings.

The different recruitment rates and seasonality of juvenile *Scarus* and *Sparisoma* may also be adaptations to differing levels of predation pressure, although predation on reef fish has not been adequately studied. Two Great Barrier Reef pomacentrids exhibited low seasonality, low recruitment, and high post-settlement survivorship, while a third species showed the reverse pattern (Sale, 1979). Juvenile *Sparisoma* may be comparable to the first group, juvenile *Scarus* to the latter. Certainly juvenile *Sparisoma* behaved differently from *Scarus*, which formed schools of 5 to 30 like-sized fish, and swam actively over the finger coral and rubble flats where they were most abundant (see Table 15, next chapter). Juvenile *Sparisoma* were more solitary. Groups generally had less than five differently-sized fish, which hovered close to cover.

In summary, juvenile scarids showed a peak in numbers during the months (June through October) when water temperatures were increasing. Recruitment was greatest in May and June of two consecutive years, the period of increased near-shore current activity, and may have been related to shifts in the positions of larvae-retaining gyres. Juvenile *Sp. aurofrenatum* showed only slight seasonal fluctuations, while *Scarus* spp. showed the most, perhaps because of differential reproductive output from pair and group spawning, or differences in survivorship of juveniles.

Adult numbers

Populations of adults were generally constant (Figures 9 to 13). Any polynomial regressions of numbers on weeks, or correlations with water temperature were weaker than those of juveniles (Tables 7 and 8). Both Iph and Tph *Sc. iserti* had stable populations at all study areas (Figure 9), *Sc. taeniopterus* showed evidence of some seasonal oscillations at sites M and B (Figure 10, Table 7), with second-order regressions there, and slight positive correlations with temperature at site P (Table 8). *Sc. vetula* showed significant second- and third-order regressions at site M (Figure 11, Table 7), and a negative correlation with water temperature (Table 8).

Adult *Sp. aurofrenatum* showed no polynomial trends at site M, but slight second-order regressions at sites B and P (Figure 12, Tables 7 and 8). *Sp. viride* revealed a linear regression, and a positive correlation with temperature at site M, a third-order regression and a negative correlation with water temperature at site P (Figure 13; Tables 7 and 8).

With such high juvenile recruitment rates at site M, particularly of *Scarus* spp., it seemed likely that similar cycles, offset from those of juveniles, would appear in adult populations as juveniles matured. However, two factors might lessen the impact of juvenile recruits on adult populations: predation, or emigration. Likewise at the offshore sites where juveniles (*Sp. aurofrenatum* excepted) were scarce, population cycles would not appear if adult immigration were constant over the year and balanced by death or emmigration. In fact, Tph newcomers did balance losses at these sites (Chapter 6).

Certain evidence supports the view that recruitment and migration contribute to adult population cycles. Adult *Sc. vetula*, the only species that oscillated seasonally at site M, were scarce offshore, and probably did not emigrate from site M. By the same token, *Sp. aurofrenatum* fluctuated offshore at sites B and P, and was the only species with appreciable numbers of juveniles there. Recruitment of adult Iph from inshore locations was also possible (Chapter 6). Likewise, *Sc. taeniopterus* populations offshore were augmented by the arrival of small Iph fish (70 to 110 mm SL), perhaps recruits from the previous year, in the summer months. I noticed the same phenomenon in 1977 and 1979, although not in 1978.

The most common scarid, *Sc. iserti* (see Table 5), did not show seasonal trends despite large recruitment. Its numbers varied seasonally in Panama (Ogden and Buckman, 1973), where food supply apparently decreases drastically in the dry season. *Sc. iserti* may have been subject to greater predation pressure than the other species due to its smaller

Figure 9. The number of Iph and Tph *Sc. iserti* counted at each study site during 1978-9. Study sites as in Figure 5.

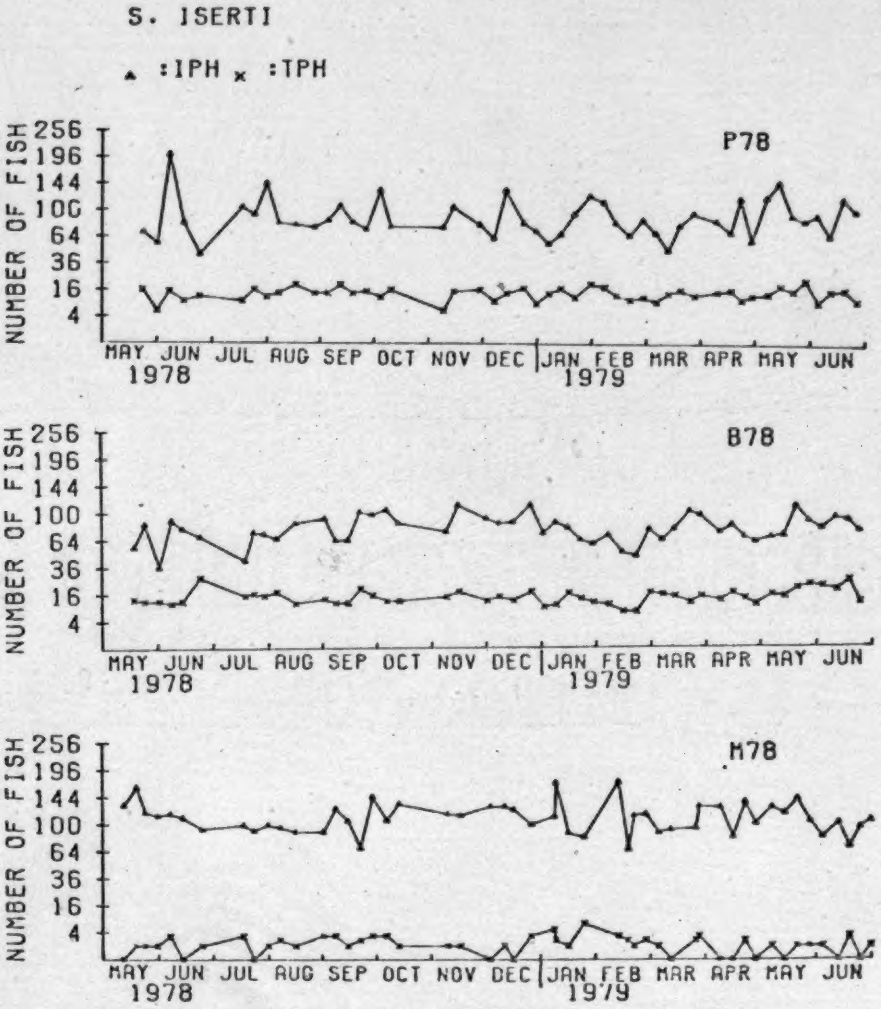


Figure 10. The number of Iph and Tph *Sc. taeniopterus* counted at each study site during 1978-9. Study sites as in Figure 5.

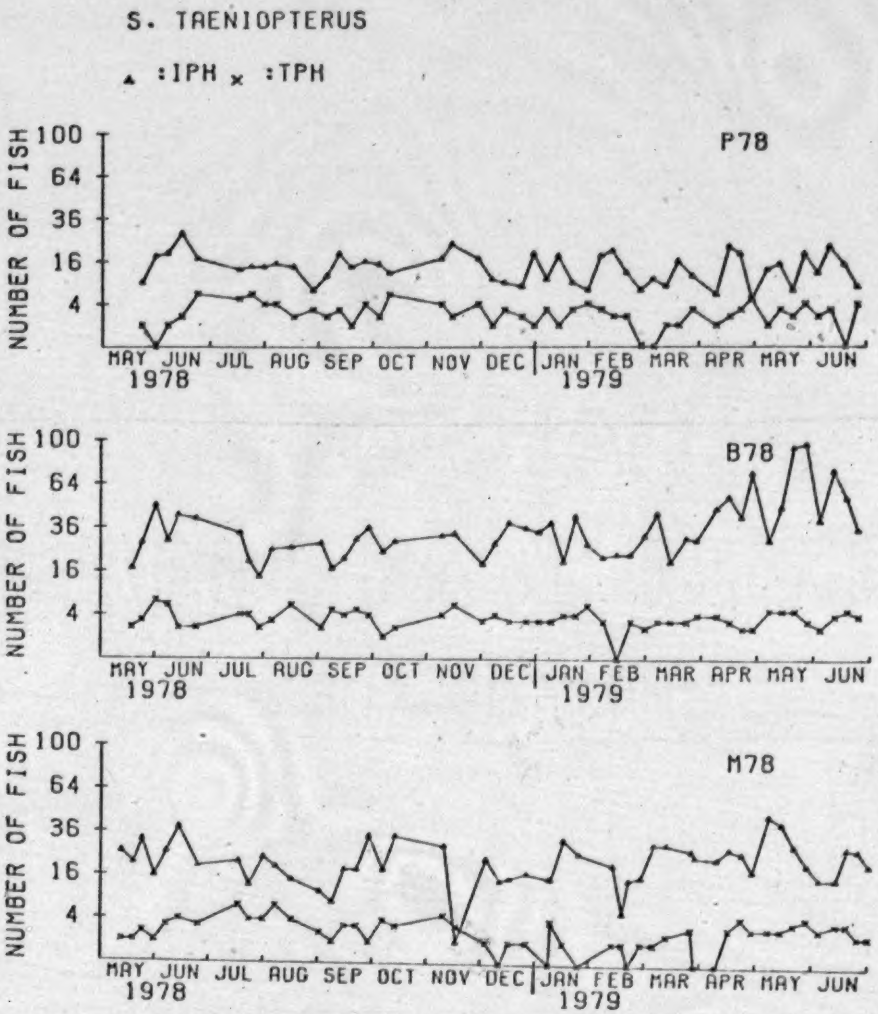


Figure 11. The number of Iph and Tph *Sc. vetula* counted at each study site during 1978-9. Study sites as in Figure 5.

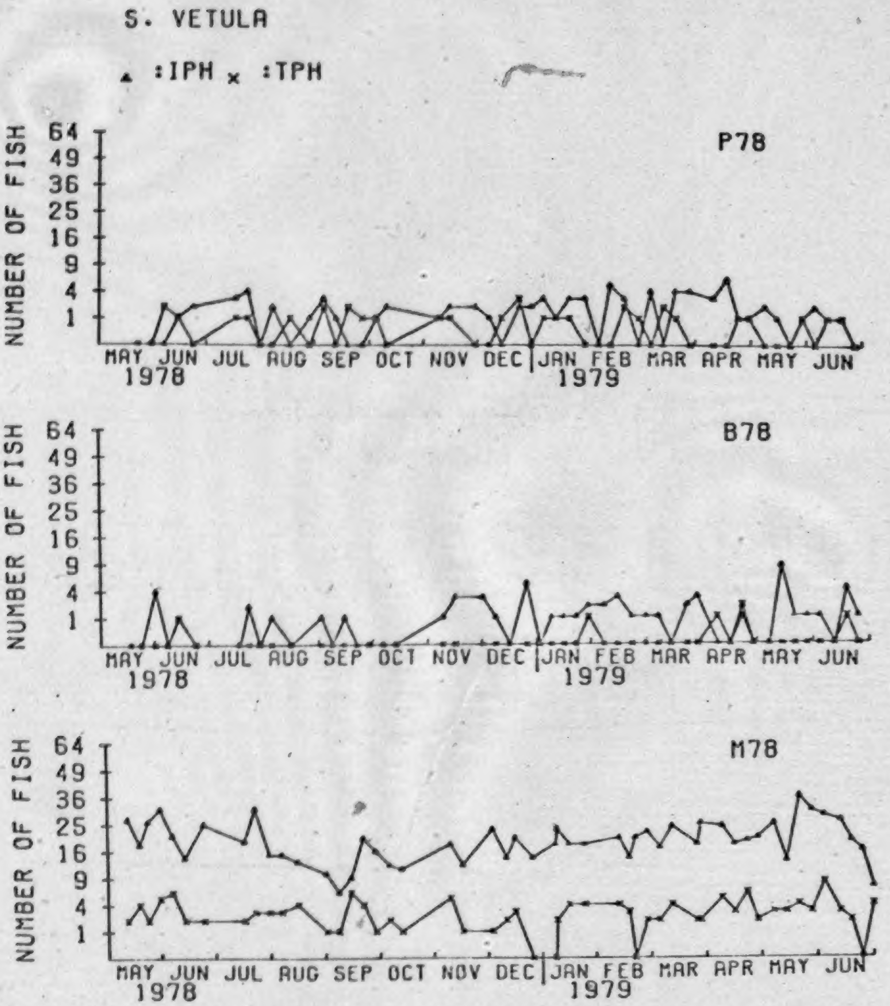


Figure 12. The number of Iph and Tph *Sp. aurofrenatum* counted at each study site during 1978-9. Study sites as in Figure 5.

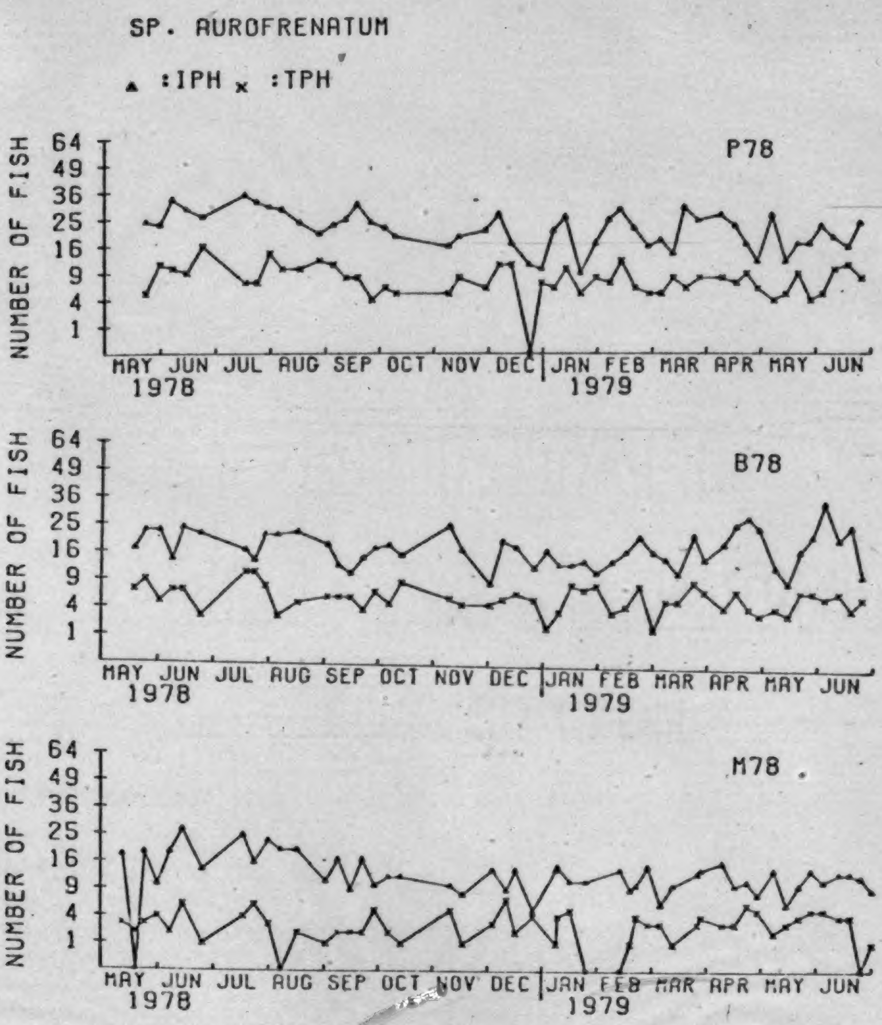
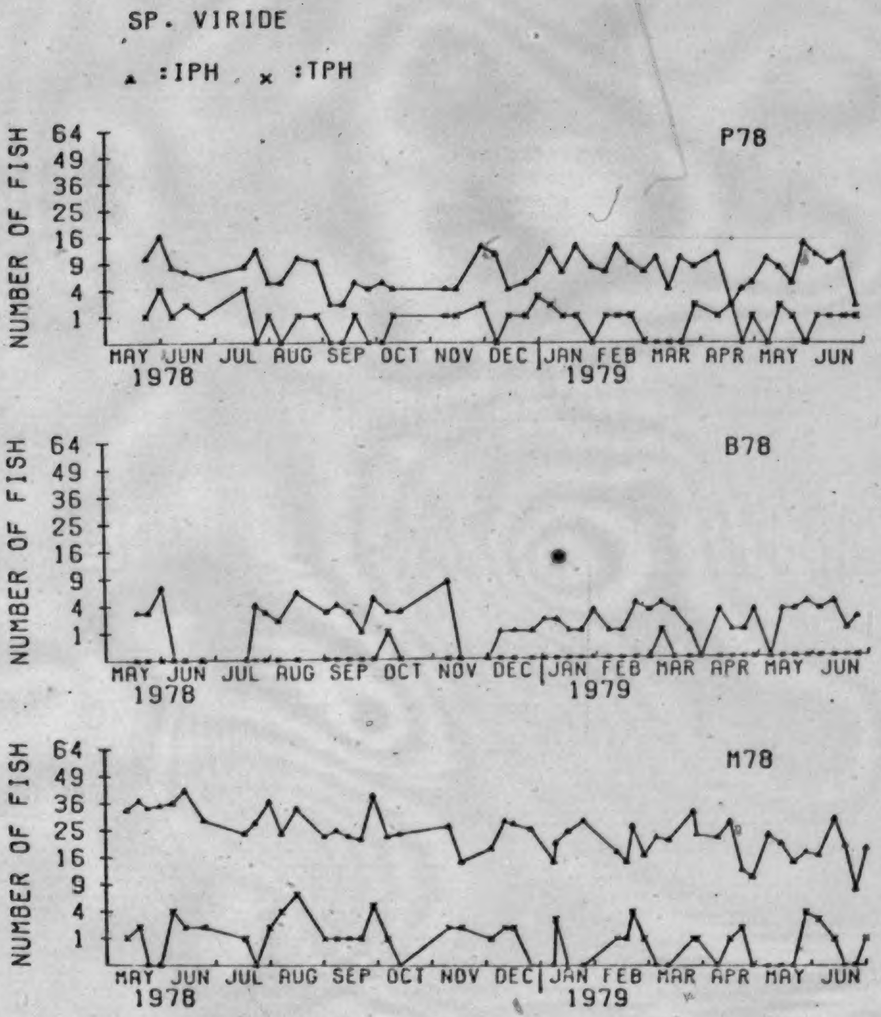


Figure 13. The number of Iph and Tph *Sp. viride* counted at each study site during 1978-9. Study sites as in Figure 5.



size, resulting in stable numbers over the year. Other reef fish adults have stable populations (e.g. Smith and Tyler, 1975; Luckhurst and Luckhurst, 1978a; Williams, 1978), and even when fluctuations in adult numbers do occur, they are of much lower order than those of juveniles (Sale, 1978a).

This type of study, like many others, is handicapped by the relatively short span of continuous observations. Many years of data collection are necessary for seasonal cycles of tropical fish to be well understood. Several researchers (Talbot et al., 1978; Sale, 1979) have made advances in this direction, although detailed information on size-frequency distribution changes throughout the year would improve our understanding of recruitment into adult populations. Future researchers should concentrate on adult reproductive output and spawning cycles, predation on juveniles, and the characteristics of larvae-retaining current gyres. Such information is crucial for resolving controversies over the stochastic nature of recruitment (e.g. Helfman, 1978; Sale, 1978b; Smith, 1978), and its impact on reef fish communities.

V. Spatial distribution patterns, social groupings and interspecific aggression

The spatial distribution patterns of coral reef fish are of particular interest since many are highly site attached. Some species associate closely with particular substrate types or reef structures (anemonefish: Moyer and Nakazono, 1978b; Fricke, 1979; other damselfish: Sale, 1972a, Clarke, 1977, Itzkowitz, 1977b; grunts: Ogden and Ehrlich, 1977; gobies: Lassig, 1977; chaetodontids: Reese, 1978, Birkeland and Neudecker, 1981; angelfish: Moyer and Nakazono, 1978a; parrotfish: Choat and Robertson, 1975). Space, rather than food, is considered to be the limiting factor on reefs and reef species show adaptions to share it (Smith and Tyler, 1972; Fishelson et al. 1974; Sale, 1975). Habitat segregation within groups of closely related reef species is often presented as evidence for niche specialization and competitive exclusion (gobies: Tyler, 1971; surgeonfish: Jones, 1968, Robertson et al., 1979; damselfish: Belk, 1975, Itzkowitz, 1977b, Robertson and Lassig, 1980; Waldner and Robertson, 1980; chaetodontids: Anderson et al., 1981). On the other hand, Sale (1974,1975,1977,1978b; Sale and Dybdahl, 1975, 1978) has argued that certain groups of reef fish overlap extensively in their habitat requirements, and that space is randomly allocated to the first juvenile or adult to claim it. The resolution of this controversy will await improved understanding of the extent of the spatial segregation on coral reefs.

Distribution patterns may be maintained by habitat selection, or by inter- and intra-specific interactions (e.g. Sale, 1972a, 1972b) The patterns that result define the social organization of a species (Brown and Orians, 1970; Reese, 1978), and set limits on its mating system (e.g. monogamous vs. polygamous; Orians, 1969, Emlen and Oring, 1977; Fricke, 1975a, 1980). It has been suggested that sex change in some coral reef fish is an adaptation to extreme site attachment (Smith, 1975; Fricke and Fricke, 1977; Fricke, 1979; Moyer and Nakazono, 1978b). Caribbean parrotfish have received only superficial ecological investigation (Robertson and Warner, 1978). Their numerical and ecological importance on reefs demands a deeper understanding of the factors controlling their spatial distribution patterns.

To investigate spatial distribution patterns and their relation to substrate features, data from grid surveys were reorganized to give the total number of each parrotfish species and phase counted in every 30 m² quadrat.[3] The surveys at sites M and B from 1976-7 and 1978-9 were analysed separately. Only results at sites M and B that were consistent in both periods were considered valid. The following substrate variables were included for analysis:

1. (only at site M) the average depths of the quadrat. None of the other study areas varied in depth, whereas site M

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[3] An initial analysis showed that the distribution of fish did not change signficantly from month to month, so lumping over the entire year was considered appropriate.

ranged from 6 m at its inshore end to 18 m offshore.

2. The percent cover in each quadrat by sand and rubble, staghorn coral, dome coral heads, finger corals, and small knob-like corals.
3. The number of damselfish: *Eupomacentrus planifrons*, *E. partitus*, and *E.* spp. (mostly *E. diencaus* and *E. variabilis*) per quadrat.

The analysis consisted of generating a correlation matrix for the parrotfish numbers and the substrate variables. In all cases Spearman rank correlation coefficients were used (Siegel, 1956). Actual coefficients are given in Appendix 1, and are summarized in the tables that follow.

The amount of distributional similarity revealed depends on the scale of the analysis (Kershaw, 1973; Robertson and Lassig, 1980). Species with apparently similar distributions on one scale could be excluding one another on a finer level. The quadrat size necessary to reveal differences depends in part on the organism's size and home range. My quadrat size of 30 m² was below the average home range size of the adults studied (see Table 25), and so interactive patterns in adult distributions were resolvable.

Correlations do not validate a causal link between two variables. Behavioural observations indicating either gregariousness or aggression between species, or experimental tests of habitat selection (e.g. Brown and Green, 1976; Reynolds, 1979) are invaluable in determining the true causes of distribution patterns.

Coefficients of dispersion

In order to measure between-quadrat variability in numbers, I calculated coefficients of dispersion (Table 9; C.D. = variance/mean; Sokal and Rohlf, 1969; Kershaw, 1973; Downhower and Brown, 1979). Although more complex indices exist (e.g. Morisita, 1971), their use was unwarranted because of their stricter assumptions. C.D.'s greater than 1.0 indicate clumped distributions, while values below 1.0 represent even distributions. Site A was excluded from the analysis due to the small number of grid surveys made there.

On average, fish at site M revealed higher C.D.'s than elsewhere. Spatial segregation was most likely there as it showed the most coral zonation (see Figure 3). Iph fish had large C.D.'s, indicating that they were localized in particular quadrats. Tph *Sp. viride* and *Sc. vetula* at site M had relatively high C.D.'s. These fish joined loose feeding aggregations of large Iph *Sp. viride* restricted to the offshore end. Iph *Scarus* had higher C.D.'s than Iph *Sp. aurofrenatum* and *Sp. viride* below 200 mm SL, which were the least gregarious parrotfish (Winn and Bardach, 1960; Barlow, 1975, Table 15 this study). Likewise, juvenile *Sparisoma* were more evenly distributed than juvenile *Scarus*, which schooled. Large changes in coral substrate occur very infrequently due to hurricanes or other disturbances (Connell, 1978). Low C.D.'s would be expected in groups whose distributions depended on behavioural interactions at

Table 9. Mean number per quadrat,standard deviation (S.D.), and coefficients of dispersion (C.D.)

SPECIES:	*Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
SITE: M YEARS: 1978 TO 1979														
MEAN	54.81	0.81	11.68	1.26	9.43	1.35	29.56	2.53	6.72	1.49	3.59	9.42	2.82	0.70
S.D.	40.40	1.12	11.65	1.35	8.56	2.51	45.14	3.83	5.60	1.43	4.63	5.48	7.11	1.64
C.D.	29.78	1.54	11.62	1.45	7.76	4.67	68.93	5.80	4.66	1.38	5.98	3.19	17.95	3.85
SITE: M YEARS: 1976 TO 1977														
MEAN	40.47	1.69	13.49	1.06	8.19	1.10	20.67	2.06	4.63	0.91	4.04	9.91	2.17	0.90
S.D.	33.82	2.14	13.50	1.62	7.77	1.77	34.15	2.55	4.03	1.22	5.15	6.03	5.69	2.26
C.D.	28.26	2.72	13.51	2.47	7.38	2.84	56.43	3.17	3.51	1.64	6.58	3.67	14.92	5.69
SITE: B YEARS: 1978 TO 1979														
MEAN	74.16	13.48	35.78	3.42	1.12	0.12	0.68	2.34	18.20	6.20	0.06	2.22	0.04	0.04
S.D.	38.60	5.00	25.08	2.79	1.19	0.33	1.25	3.16	6.51	2.79	0.24	1.76	0.28	0.20
C.D.	20.09	1.86	17.58	2.28	1.26	0.90	2.31	4.27	2.33	1.26	0.96	1.40	2.00	0.98
SITE: B YEARS: 1976 TO 1977														
MEAN	20.86	5.58	12.40	1.68	0.12	0.02	0.26	1.48	7.32	2.94	0.02	0.78	0.08	0.0
S.D.	9.28	3.09	8.95	1.24	0.33	0.14	0.69	1.45	4.16	1.96	0.14	0.89	0.27	0.0
C.D.	4.13	1.71	6.45	0.91	0.90	1.00	1.85	1.41	2.36	1.31	1.00	1.01	0.94	0.0
SITE: P YEARS: 1978 TO 1979														
MEAN	83.62	13.30	13.12	2.40	1.56	0.56	2.46	3.80	20.44	7.26	0.08	5.72	1.48	0.86
S.D.	34.08	4.78	7.16	1.62	1.54	1.11	3.82	2.75	6.88	3.08	0.27	3.00	1.47	1.03
C.D.	13.89	1.72	3.91	1.09	1.52	2.20	5.93	1.99	2.32	1.30	0.94	1.58	1.47	1.23

territorial borders which could change more rapidly than reef structure. Strong correlations between some environmental factor and fish numbers would be especially likely in species with high C.D.'s.

A. Comparisons between 1976-7 and 1978-9

To test for between-year constancy in distribution patterns, I calculated correlations between numbers of parrotfish seen in quadrats during 1976-7 and 1978-9 at sites M and B. For all species the coefficients at site M were highly significant (*Sc. iserti*, r = 0.78; *Sc. taeniopterus*, r = 0.71, *Sc. vetula*, r = 0.65, *Sp. aurofrenatum*, r = 0.59; *Sp. viride*, r = 0.59; juvenile parrotfish r = 0.69; for all, P < 0.001, n = 100) indicating that spatial distribution patterns there were relatively stable. Correlations between years at site B were lower (*Sc. iserti*, r = 0.09, ns; *Sc. taeniopterus*, r = 0.29, P < 0.025; *Sp. aurofrenatum*, r = 0.49, P < 0.001, n = 50). Site B was more homogeneous than site M, and strong attachments of species to particular regions were less likely to occur. Nevertheless, spatial distribution patterns appeared to be stable over the nearly three-year span of the study.

B. Correlations with depth at site M

I examined possible depth segregation of species at site M with further correlations (Table 10). Tph *Sc. iserti*, Iph and Tph *Sc. taeniopterus*, Iph *Sp. aurofrenatum*, and

Table 10. Summary of significant ($P < 0.05$) Spearman's correlations between number of parrotfish per quadrat and substrate variables, including depth, at site M. Variables are % cover by each substrate type. If no phase is indicated, correlation applies to both Iph and Tph fish. See Appendix 1A for details.

Variables:	Positive correlations	Negative correlations
Depth	Tph *Sc. iserti* *Sc. taeniopterus* Iph *Sp. aurofrenatum* Large Iph *Sp. viride* Tph *Sp. viride*	Iph *Sc. vetula* Juv *Sp. viride*
Sand	Tph *Sc. vetula*	
Rubble	Iph *Sc. iserti* Iph *Sc. taeniopterus* Juv & Iph *Sp. aurofrenatum* Small Iph *Sp. viride*	
Large heads		Iph *Sp. aurofrenatum*
Small heads		Iph *Sc. taeniopterus* Juv *Scarus* Juv & Iph *Sp. aurofrenatum*
Staghorn coral	Iph *Sc. vetula*	Iph *Sc. iserti* Iph *Sc. taeniopterus* Juv & Iph *Sp. aurofrenatum*
Finger coral	Iph *Sc. taeniopterus* Juv *Scarus* Juv & Iph *Sp. aurofrenatum* Juv *Sp. viride*	
Dead coral	Tph *Sc. taeniopterus*	Juv *Scarus* Juv & Iph *Sp. aurofrenatum* Juv *Sp. viride*

large Iph and Tph *Sp. viride* were more abundant in deeper water. Iph *Sc. vetula* and juvenile *Sp. viride* were negatively correlated with depth. In 1978-9, juvenile *Scarus* were negatively correlated with depth, while juvenile *Sp. aurofrenatum* were positively so, and the trend, although not quite significant, held in 1976-7 as well.

A correlation with depth could be due to the effects of another intervening variable, like coral type, itself related to depth. This did occur for a few substrate variables. Small coral heads, staghorn coral, and the damselfish *Eupomacentrus planifrons* were negatively correlated with depth ($r = -0.23$, $P < 0.01$; $r = -0.39$, $P < 0.001$; $r = -0.55$, $P < 0.001$, respectively), while the damselfish *E. partitus* correlated positively ($r = 0.40$, $P < 0.001$). A partial correlation analysis (Snedecor and Cochrane, 1980) was used to test for the effects of these variables on the number of parrotfish in a quadrat (see next section).

Initial phase *Sc. vetula* were not restricted to areas as shallow as site M for they migrated into deeper water at sunset (Dubin and Baker, 1981). Dives to 40 m revealed only *Sp. aurofrenatum*, *Sc. iserti*, and *Sc. taeniopterus*, of which the last was most abundant. With the exception of *Sc. taeniopterus*, these species were found in water as shallow as 3 m in other parts of Barbados (pers. obs.; Frydl and Stearn, 1978). However, depth segregation within site M of some species did occur.

C. Correlations with substrate variables

Site M

As the analysis of coefficients of dispersion predicted, Iph and juveniles showed more correlations with substrate variables than did Tph (Table 10). This could occur if, because of their smaller size, Iph and juveniles were more dependent on certain types of cover for protection. Alternatively, their greater energy requirements for egg production and growth may tie Iph and juveniles to particularly rich food sources found on certain substrate types. However as Choat and Robertson (1975) reported, numbers were not generally correlated with the percent cover by dead coral, a primary food source.

With the exception of Iph *Sc. vetula*, there were no clear divisions of species on the basis of their relations with substrate variables (Table 10). Iph *Sc. vetula*, and possibly Tph *Sp. aurofrenatum* were the only parrotfish to show positive correlations with percent cover by staghorn coral.[4] Iph of the three species common at the barrier reef sites, *Sc. iserti*, *Sc. taeniopterus*, and *Sp. aurofrenatum*, shared several correlations: positive ones with rubble and finger coral, and a negative one with staghorn coral. This indicated a certain degree of ecological similarity in these species. Juvenile and Iph generally showed similar substrate correlations, particularly *Sp. aurofrenatum*, the only species with juveniles common throughout the adults' range. This species had more correlations with substrate variables than any other. My results concur with Barlow's (1975) observations that *Sp. aurofrenatum* is closely tied to coral substrate.

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[4] With depth controlled in a partial correlation analysis, the relationship between Tph *Sp. aurofrenatum* and staghorn coral became significantly positive.

Juvenile parrotfish did not share identical substrate correlations, although all were positively correlated with finger coral and negatively correlated with small coral heads (Table 10). Finger coral may offer cover, and be too finely branching to conceal predators. Small coral heads may have opposite properties. It is unknown whether juveniles actively select these substrates, or are forced into them by predation or aggression from other fish. Information on the behaviour of recruits, only now entering the literature (D. Williams, 1980; Sale et al., 1980) will do much to advance our understanding of habitat selection by reef fish.

Although the coefficients of dispersion of large Iph and Tph *Sp. viride* indicated a high degree of clumping, these fish correlated consistently only with depth. This species ranged widely over diverse substrate types (pers. obs; Frydl, 1979), and its large size probably freed it from dependence on cover for protection from predation (Choat and Robertson, 1975).

This analysis revealed that, Iph *Sc. vetula* excepted, there were few obvious constrasts among species in substrate correlations at site M. The general impression that parrotfish have widely defined ecological requirements with large amounts of interspecific overlap (Choat, 1969; Choat and Robertson, 1975) is upheld by my results.

Site A

There were fewer correlations with substrate variables at site A, but those that did exist agreed with those at site M (Table 11). Iph *Sc. vetula*, was again most abundant in staghorn coral. Juvenile scarids were not abundant in areas with coral heads, but were positively correlated with low relief substrates such as sand and rubble or finger coral.

Sites B and P

There were few clearly consistent trends in correlations with substrate variables at sites B and P (Table 12). Iph *Sp. aurofrenatum* were positively correlated with percent cover by sand. Perhaps this rather solitary species (see Table 15), actively avoids predator-concealing corals, while the *Scarus* species derive protection from aggregating (Itzkowitz, 1974).

D. Correlations with damselfish numbers

Site M

There was clear spatial segregation among damselfish present at site M, with *E. planifrons* most abundant in staghorn coral ($r = 0.74$, $P < 0.001$). Williams (1978) found a similar trend. *E. partitus* was most common in finger coral ($r = 0.48$, $P < 0.001$) and rubble ($r = 0.38$, $P < 0.001$), and

Table 11. Summary of significant ($P < 0.05$) Spearman's correlation coefficients between number of parrotfish per quadrat, and substrate variables at site A. Variables are percent cover by substrate types. See Appendix 1B for details.

Variables:	Positive correlations	Negative correlations
Sand & rubble	Juv *Sp. aurofrenatum*	Iph *Sc. taeniopterus* Iph *Sc. vetula*
Large heads		Juv *Scarus*
Staghorn coral	Iph *Sc. vetula*	Juv *Sp. aurofrenatum*
Finger coral	Juv *Scarus*	
Dead coral	Iph *Sc. taeniopterus* Iph *Sc. vetula*	Juv *Scarus*

Table 12. Summary of significant ($P < 0.05$) Spearman's correlation coefficients between number of parrotfish per quadrat and substrate variables at sites B and P. Variable is percent cover by sand. See Appendix 1C for details.

Variable:	Positive correlations	Negative correlations
Sand and rubble		
Site B	Iph *Sp. aurofrenatum*	
Site P	Juv *Sp. aurofrenatum* Iph *Sp. aurofrenatum*	Iph *Sc. vetula* Tph *Sp. aurofrenatum*

other *Eupomacentrus* species in the rubble and small coral head zone ($r = 0.44$, $P < 0.001$). Clarke (1977), Itzkowitz (1977b), and Waldner and Robertson (1980) found habitat segregation among these species elsewhere in the Caribbean.

Juveniles and Iph were more often negatively correlated with damselfish than were Tph (Table 13). Iph *Sc. vetula* were the only parrotfish to correlate positively with *E. planifrons* (although Tph *Sp. aurofrenatum* did so in 1978-9), perhaps a result of these species' attachment to staghorn coral. Juvenile *Scarus*, juvenile and Iph *Sp. viride* and all Tph scarids showed no consistent correlations. [5] Iph *Sc. iserti*, *Sc. taeniopterus*, and juvenile and Iph *Sp. aurofrenatum* were negatively correlated with this damselfish. All correlations with *E. partitus* and parrotfish were positive, and were probably a result of these species' similar substrate associations. Tph *Sc. iserti* associated positively with the other *Eupomacentrus* species, Iph *Sc. vetula*, and juvenile *Scarus*, negatively.

Site A

At site A only juvenile *Scarus* and juvenile *Sp. aurofrenatum* were negatively associated with *E. planifrons* numbers, and there were no significant associations with *E. partitus* (Table 13). Other *Eupomacentrus* species were too sparse to be tested. Tph *Sp. aurofrenatum* were positively correlated with *E. planifrons*. As at site M, *E. planifrons*

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[5] With the effects of depth controlled in a partial correlation analysis, a negative correlation between *E. planifrons* and large Iph and Tph *Sp. viride* disappeared.

Table 13. Summary of significant ($P < 0.05$) Spearman's correlations between number of parrotfish and number of damselfish per quadrat. See Appendix 1D for details.

Damselfish	Positive correlations	Negative correlations
E. planifrons:		
Site M	Iph *Sc. vetula*	Iph *Sc. iserti* Iph *Sc. taeniopterus* Juv & Iph *Sp. aurofrenatum*
Site A	Tph *Sp. aurofrenatum*	Juv *Scarus* Juv *Sp. aurofrenatum*
Site B		Iph *Sp. aurofrenatum*
Site P	Iph *Sc. vetula* Tph *Sp. aurofrenatum*	Juv *Sp. aurofrenatum*
E. partitus:		
Site M	Iph *Sc. iserti* Iph *Sc. taeniopterus* Juv *Scarus* Juv & Iph *Sp. aurofrenatum* Small Iph & Tph *Sp. viride*	
Site A	none	
Site B	Iph & Tph *Sc. iserti*	
Site P	Iph *Sc. vetula* Large Iph *Sp. viride*	
Eupomacentrus spp.:[1]		
Site M	Tph *Sc. iserti*	Iph *Sc. vetula* Juv *Scarus*

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[1] sufficient numbers only at site M.

were associated positively with staghorn coral (r = 0.45, P < 0.001), but *E. partitus* showed no clear substrate correlations.

Sites B and P

At site B, *E. planifrons* correlated negatively only with Iph *Sp. aurofrenatum*, at site P, only with juvenile *Sp. aurofrenatum* (Table 13). Iph *Sc. vetula* and Tph *Sp. aurofrenatum* showed positive correlations at site P. There were no indications at this scale of analysis of habitat segregation between the damselfish species. Both correlated negatively with percent cover by sand (*E. planifrons*: r(site B) = -0.50, r(site P) = -0.54, P < 0.001; *E. partitus*: r(site B) = -0.28, r(site P) = -0.31, P < 0.05). At site B, *E. partitus* correlated positively with both Iph and Tph *Sc. iserti*; at site P, with Iph *Sc. vetula* and large *Sp. viride*. The densities of other *Eupomacentrus* species were too low to allow testing of their correlations with parrotfish numbers.

Effects of damselfish on parrotfish spatial distribution patterns

E. planifrons may have had a considerable impact on the distribution of certain parrotfish, particularly at site M. This species' high levels of aggression, and well-developed interspecific territoriality are primarily a defence against food competitors, especially parrotfish (Myberg and Thresher, 1974; Thresher, 1976a, 1976b, 1977a, 1978b, 1979b; Robertson et al., 1976; Itzkowitz, 1974, 1979; Williams, 1979, 1980). The other *Eupomacentrus* species are less aggressive than *E. planifrons* (Thresher, 1977a), although they too defend interspecific territories. *E. leucostictus* and *E. variabilis* direct a large proportion of their attacks towards parrotfish (Ebersole, 1977; Gronell, 1980), but were too uncommon on my study areas to have a signficant effect on parrotfish. Although very abundant, *E. partitus* attacks parrotfish rarely, and is most aggressive towards wrasses (Myrberg, 1972). Most of its correlations with scarid numbers were positive, a result of similar substrate associations. The aggressive behaviour of *E. diencaus* is not well known, as it was only recently distinguished from the other dusky damselfish *E. fuscus* and *E. dorsopunicans* (Greenfield and Woods, 1974). Attacks on parrotfish by this last species have been described (Ogden and Buckman, 1973; Itzkowitz, 1974), but it was not found on my study areas. *E. fuscus* also attacks parrotfish (Barlow, 1975; Mochek, 1975), but it is not clear which dusky damselfish was involved. My observations indicate that the great bulk of damselfish attacks on parrotfish came from *E. planifrons*.

The present analysis shows that the distributions of small parrotfish, particularly juveniles and Iph, are most affected by *E. planifrons*. Their smaller size may make them easier to dominate (Constanz, 1975; Waldner and Robertson, 1980; Robertson and Lassig, 1980). *Sc. iserti* below 70 mm SL were attacked more frequently by *E. planifrons* in Panama than were larger fish (Robertson et al., 1976). While *E. planifrons* did occasionally chase off larger Tph fish in

Barbados, Iph fish received more attacks (Chapter 7). Robertson et al. (1976) reported no difference in the rate of attacks on Iph and Tph *Sc. iserti*. However, Iph and Tph fish in his study fed at equivalent rates. These authors showed a positive relation between scarid feeding rate and the attack rate by *E. planifrons*. Iph fish all fed at greater rates than Tph in Barbados (Chapter 7). Damselfish may preferentially chase Iph and juveniles because of their greater potential competitive impact. A study to this effect, using the model bottle method of Myrberg and Thresher (1974) would be most revealing.

Iph *Sc. vetula*, and possibly Tph *Sp. aurofrenatum*, showed positive correlations with *E. planifrons* numbers. Neither species was immune to attacks from damselfish, however, and it is unclear how they manage to remain among dense *E. planifrons* groups. It would be very informative to compare *Sc. vetula - E. planifrons* interactions with those of other scarids.

The aggressive responsiveness of *E. planifrons* throughout its depth range is also worth investigation. Site A parrotfish showed fewer negative correlations than site M fish with *E. planifrons* numbers, even though the average densities of damselfish were similar (Table 3). The small number of grid surveys at site A, and the narrower range of damselfish densities there could have reduced the sensitivity of this analysis. However, those site A species studied did receive fewer damselfish attacks than site M fish (see Chapter 7). Emery (1973) stated that *E. planifrons* became weakly territorial and wandered in the deeper portions of its range. Site A was relatively deep (15 to 25 m), and although I did not notice a marked difference in damselfish behaviour there, they may have been less efficient at expelling parrotfish.

Interactions with damselfish were probably responsible for the negative correlations of some species with staghorn coral. Removal experiments have shown that parrotfish will rapidly invade and feed in emptied damselfish territories (Low, 1971; Robertson et al., 1976). While some scarids may actively select certain substrate types (e.g. Iph *Sc. vetula* and staghorn coral), most species existed over widely different coral types, unless restricted to certain ones by the aggression of territorial damselfish.

E. Correlations among parrotfish

Interactions among parrotfish could also affect their distribution patterns. The relatively even distributions of many Tph species were perhaps due to the spacing-out effect of their territorial interactions. In this section I will deal with interactions between species or phases. Intra-phase aggression is discussed in Chapter 7. To test for interspecific or inter-phase distributional associations, I looked for positive or negative correlations among pairs of species (Table 14), along with the number of times that pairs were seen together (Table 15) and the number of aggressive interactions between them (Table 16). Such a correlative approach tests for interactions and ecological specializations of groups of reef fish (Sale and Dybdahl, 1975; Talbot et al., 1978). No correlation indicates either unsystematic differences in substrate requirements or simply no specific requirements. It also means that strong cohesiveness or repulsion between members of a pair is unlikely. Positive correlations indicate that pairs share similar substrate requirements, and possibly form cohesive groups. Behavioural observations (Table 15) would verify this latter possibility. Negative interactions could indicate that pairs have opposing substrate requirements or exclude one another through competitive interactions. Behavioural observations, or selective removal experiments are necessary to confirm competitive exclusion (e.g Hixon, 1980a; Larson, 1980a).

Correlations between conspecifics

Correlations between conspecifics were rarely negative, with the exception of those between some Tph fish and juveniles (Table 14). Aggressive interactions between Tph and juveniles were rare, so these differences represented habitat (mainly depth) segregation rather than competitive exclusion. Conspecifics of different phase did not show pronounced spatial segregation. Positive correlations appeared among Tph-Iph pairs which often aggregated (Table 15): *Sc. iserti* at all but site P and *Sp. viride* at sites M and P. Iph-juvenile correlations were

Table 14. Summary of Spearman's correlation matrix between number of parrotfish per quadrat. Significant correlations (P < 0.05) at each site are shown. 'M' stands for site M, etc. Negative correlations are preceded by a minus sign and are underlined.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	--													
Tph	M,A,B	--												
Sc. taeniopterus														
Iph	M,A		--											
Tph	A,-P	M,A,P	M	--										
Sc. vetula														
Iph					--									
Tph		P				--								
Scarus juv.	M,A,B		A		M		--							
Sp. aurofrenatum														
juv.	M,A		M,A				M,A,B	--						
Iph	M,P	M,A	M	-P	-P			M	--					
Tph			-A	M	P		-A	-P		--				
Sp. viride														
juv.	M				M	-M	M	M			--			
Iph-small	M				M		M			-B		--		
Iph-large			M	M		M	P		M	M	-M		--	
Tph			M	M		M		-P	M	M	-M	P	M	--

found among some *Scarus* species and *Sp. aurofrenatum* as a result of both gregariousness (Table 15) and and similar substrate correlations (Tables 10 to 13).

Correlations between different parrotfish species

There were few indications of negative interspecific associations at site M (Table 14). Iph *Sc. vetula* differed most from the other parrotfish. *Sc. iserti*, *Sc. taeniopterus*, *Sp. aurofrenatum* and *Sp. viride* all correlated positively with one another. *Sc. vetula* did so only with groups that, like itself, were uncommon on the barrier reef: juvenile *Scarus* and both juvenile and Iph *Sp. viride* (Table 14). Juvenile parrotfish showed strong positive correlations, particularly juvenile *Scarus*with juvenile *Sp. viride*. Tph had fewer interspecific correlations than Iph. However, Tph *Sc. iserti* were positively correlated with Tph *Sc. taeniopterus*, which were positively correlated with Tph *Sp. aurofrenatum*. Tph *Sc. vetula* and both adult phases of *Sp. aurofrenatum* and *Sc. taeniopterus* correlated positively with Tph and large Iph *Sp. viride*, occasionally joined their feeding aggregations (Table 15), and were more numerous in the offshore, deeper end of site M where the aggregation wandered.

The only interspecific negative correlations were between Tph *Sc. vetula* with juvenile *Sp. viride*.[6] This was certainly due to different substrate requirements rather than competitive interactions, since aggression between this pair was never seen. The lack of negative correlations and the large number of positive ones at site M, reinforced the conclusion that strong differences in spatial distribution were not apparent on this scale of analysis and indeed, that many species shared similar distribution patterns.

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[6] With depth controlled in a partial correlation analysis, a negative correlation between Tph *Sp. viride* and Iph *Sc. vetula* disappeared.

There were fewer interspecific correlations at site A and only two were negative: Iph *Sc. taeniopterus* and juvenile *Scarus*, both with Tph *Sp. aurofrenatum* (Table 14). Tph *Sp. aurofrenatum* occasionally chased Iph *Sc. taeniopterus* (Table 16), so spatial segregation due to competitive interactions was possible although unlikely as this particular correlation did not appear at the other sites. Juveniles correlated with each other, as did Iph *Sc. iserti* with *Sc. taeniopterus*, and Tph *Sc. iserti* with Tph *Sc. taeniopterus* and Iph *Sp. aurofrenatum*.

At sites B and P there were also fewer significant correlations than at site M (Table 14). Both Iph and Tph *Sc. iserti* positively correlated with juveniles, as did juveniles with each other at site B. Iph *Sc. iserti* and *Sc. taeniopterus* showed positive correlations. A negative correlation between Tph *Sp. aurofrenatum* and small Iph *Sp. viride* was noted, perhaps evidence of avoidance since Tph *Sp. aurofrenatum* commonly chased *Sp. viride* (Table 16). At site P, Tph *Sc. taeniopterus* correlated positively with Tph *Sc. iserti* and *Sc. vetula*, but negatively with Iph *Sc. iserti* and *Sp. aurofrenatum*, all of which it occasionally

Table 15. Percent of time that parrotfish were seen swimming or feeding within one to three body lengths of at least one other parrotfish during grid surveys (TOTAL PERCENT). The percent of the total sightings with each species are given. Values are averaged over all sites. Total sightings in parentheses.

		SEEN WITH: *Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
	TOTAL PERCENT:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Iph *Sc. iserti* (18790)	69.3	61.8	7.6	17.0	0.04	3.5	0.03	3.6	3.7	6.7	0.1	0.3	2.0	0.03	0.01
Tph *Sc. iserti* (930)	22.9	14.1	2.0	6.1	0.0	0.7	0.0	0.3	0.1	1.2	0.03	0.0	0.3	0.0	0.0
Iph *Sc. taeniopterus* (5776)	56.6	23.3	2.3	46.3	0.5	2.3	0.1	2.5	4.1	5.6	0.1	0.7	1.7	0.1	0.1
Tph *Sc. taeniopterus* (643)	6.7	1.0	0.0	4.2	1.0	0.4	0.2	0.0	0.0	0.1	0.2	0.0	1.2	0.2	0.2
Iph *Sc. vetula* (1946)	30.0	9.4	0.8	3.0	0.1	18.9	0.8	0.2	2.5	0.2	1.3	0.03	0.3	1.8	0.03
Tph *Sc. vetula* (291)	4.4	0.4	0.0	0.3	0.2	1.4	0.8	0.0	0.0	0.1	0.1	0.0	0.6	1.4	0.5
juv. *Scarus* (5337)	74.7	5.3	0.2	8.6	0.0	2.3	0.0	62.1	25.8	1.2	0.0	7.5	0.8	0.0	0.0
juv. *Sp. aurofrenatum* (897)	43.0	5.3	0.3	8.4	0.0	0.6	0.0	20.6	21.3	2.1	0.0	3.0	0.2	0.0	0.0
Iph *Sp. aurofrenatum* (3554)	22.8	11.0	0.6	8.6	0.1	1.1	0.03	0.6	1.1	8.0	1.2	0.1	2.2	0.1	0.03
Tph *Sp. aurofrenatum* (1098)	11.7	0.4	0.0	0.4	0.2	0.2	0.1	0.0	0.0	2.9	6.5	0.0	1.5	0.2	0.3
juv. *Sp. viride* (793)	28.1	4.9	0.0	2.0	0.0	0.5	0.0	19.6	9.4	0.2	0.0	6.7	0.4	0.0	0.0
Iph *Sp. viride*: small (2438)	15.1	4.5	0.1	3.3	0.8	1.1	0.1	0.3	0.1	2.8	0.9	0.2	6.7	0.2	0.0
Iph *Sp. viride* :large (582)	27.6	0.5	0.0	3.3	0.6	1.1	2.2	0.0	0.0	0.5	1.0	0.0	1.5	23.1	12.1
Tph *Sp. viride* (210)	16.7	0.2	0.0	1.0	0.8	0.6	1.6	0.0	0.0	0.5	1.1	0.0	3.2	11.9	8.7

Table 16. Interspecific aggression: total number of aggressive interactions seen during 155 hours of observation.

SPECIES RECEIVING ATTACK:	*Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES INITIATING ATTACK:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Iph *Sc. iserti*			8		1									
Tph *Sc. iserti*			31	4	8									
Iph *Sc. taeniopterus*	5	1			2									
Tph *Sc. taeniopterus*	8	15			13				2					
Iph *Sp. aurofrenatum*	3	1	3									3		
Tph *Sp. aurofrenatum*	3	6	7	4	3							24		

attacked (Table 16). Iph *Sc. taeniopterus* correlated positively with both large Iph and Tph *Sp. viride*.

Social groupings and interspecific aggression

Positively correlated species were probably not excluding one another within a quadrat. Parrotfish commonly formed heterospecific groupings (Table 15; Ogden and Buckman, 1973; Itzkowitz, 1974, 1977a). Such loose feeding aggregations were especially common at site M (Appendix 1F). Those fish that showed positively correlating spatial distribution patterns (e.g. Iph *Sc. iserti*, *Sc. taeniopterus*, and *Sp. aurofrenatum*), often swam and fed together (Table 15). Interspecific aggression was noted in less than 0.5 % of the grid survey sightings. Activity budgets (Chapter 7) gave similarly low values. In over 150 hours of intensive behavioural observations, I saw fewer than 180 interspecific interactions (Table 16), and many of these were of low intensity, e.g. supplanting at a food source (see also Barlow, 1975). The possibility that a fish's presence alone sufficed to repel other species was not tested, but seemed unlikely given their gregariousness.

Parrotfish generally attacked fish that were the same size, or smaller than themselves. Tph *Sc. iserti* chased off Iph *Sc. taeniopterus* more often than any other parrotfish, yet the two correlated positively at sites M and A. Likewise Tph *Sc. taeniopterus* chased Tph *Sc. iserti*, with which it correlated positively at all but site B. It also chased Iph *Sc. vetula*, and received aggression from it in return. A size-dependent interspecific dominance network may exist among the scarids inhabiting particular sites, but it was not highly enough developed to lead to exclusive use of space and interspecific territoriality of the sort that exists in certain Great Barrier Reef damselfish (Sale, 1974, 1975).

F. Summary and discussion

Correlation coefficients at the offshore sites A, B, and P were less often significant, and significant ones were lower than those at site M where over half had probability levels below 0.001 (Appendix 1). This result is consistent with the analysis of coefficients of dispersion, and correlations with substrate variables, which showed that clumping and substrate segregation were higher at site M than elsewhere.

While some depth segregation occurred at site M, it probably reflected the effects of underlying variables such as damselfish distributions. *Sc. vetula*, and possibly *Sp. viride* may have been restricted to more shallow water than the other species. *Sc. vetula* differed most from the other scarids in being positively associated with staghorn coral and the damselfish *E. planifrons*. *Sp. viride* was intermediate, showing correlations that linked it to both *Sc. vetula* and the other species. Interestingly, *Sp. viride* was more common at the offshore sites than *Sc. vetula* (see Table 5), and may have been more similar in substrate associations to the other species.

Juveniles of all species showed positive correlations with finger corals, and negative ones with small coral heads, possibly indicating avoidance of concealed predators. Those species most common at the offshore sites, Iph *Sc. iserti*, *Sc. taeniopterus*, and juvenile and Iph *Sp. aurofrenatum*, shared numerous correlations with substrate variables. Iph had more correlations than Tph, an indication of their greater dependence on coral for protection or food.

The damselfish, *Eupomacentrus planifrons*, may be the single most important factor affecting the distributions of juvenile and Iph parrotfish, particularly at site M. Its lesser effects on Tph fish and Iph *Sc. vetula* may be due to their greater size, which renders them more difficult to dominate. There were fewer correlations at the other study sites. Iph *Sp. aurofrenatum* showed the only consistent correlations at the more homogeneous offshore sites B and P, being positively correlated with percent cover by sand.

There were few striking positive or negative associations between parrotfish. Juveniles tended to occur in the same areas, and were more often positively correlated with Iph than with Tph parrotfish, a reflection of both similar substrate relations, and greater gregariousness. Negative correlations were uncommon, and could be related to actual aggressive interactions in only a few cases (e.g. Tph *Sp. aurofrenatum* chasing off *Sp. viride* at site B). Negative correlations between Tph and juveniles at site M were the result of depth segregation. Groups of parrotfish that had shown similar substrate associations were often positively correlated, and tended to aggregate. Interspecific aggression among parrotfish occurred infrequently, and could not account for the spatial segregation that did occur.

These results appear to support Sale's (op. cit.) view of reef fish as generalists. Only Iph *Sc. vetula* showed clear contrasts with the other species, and is worthy of more detailed study than it has received so far. The other species emerge from this analysis, not with precisely defined, distinct ecological requirements, but with a multitude of overlapping associations. While parrotfish overall may be considered as specialized herbivores, certain groups of species (e.g. *Sc. iserti*, *Sc. taeniopterus*, and *Sp. aurofrenatum*), are very similar in their habitat requirements. The fact that there was a different blend of these species at each site - e.g. more *Sc. taeniopterus* at site A, more *Sp. aurofrenatum* at site P - may reflect subtle ecological differences between these species which this analysis did not reveal. An analysis of their space utilization and feeding behaviour (Chapter 7) will examine whether these do show resource specializations not revealed here. The search for one single factor controlling species' distribution patterns on coral reefs may be futile; reef fish appear to be adapted to exploiting a complex and variable habitat. I suggest that future researchers interested in understanding the spatial distribution patterns of reef fish continue with detailed correlative studies such as this one, or experiment on habitat selection, particularly by juvenile fish.

VI. Parrotfish life history

It is now well established that many fish species reside relatively permanently in home areas. Early tagging studies revealed that some reef species were long-term residents with good homing ability (Bardach and Menzel, 1956; Bardach, 1958; Randall, 1961b; Springer and McErlean, 1962a). Parrotfish occupy certain reef areas for at least several months and home when displaced (Winn et al., 1964; Ogden and Buckman, 1973; Buckman and Ogden, 1973; Bruce, 1978). Usually the occupancies reported are minimum values; the study often ends before any turnover of individuals has occurred (Reese, 1973).

By observing individual turnover in natural populations over a period of time, it is possible to determine the underlying processes of population dynamics, the stages an individual passes through as it progresses from juvenile to adult. Such stages, or behavioural classes, separable on the basis of site-attachment, aggression or reproductive activities, are known for many fish species, including *Sc. iserti* (Warner and Downs, 1977), but have not been identified in other parrotfish.

I was able to determine the occupancy times of parrotfish continuously from May, 1978 to July, 1979 at sites M, B and P. Site A was monitored for only two months, so occupancy of its residents was unknown. In some cases, fish that had been identified in 1976-7 were still present in 1978. I had more success with some groups than others.

Tph *Sp. aurofrenatum* and *Sc. taeniopterus* were recognizable at a glance with great certainty over long periods of time. Tph *Sc. iserti* were more difficult as they were numerous, and their color marks were less well defined; a positive identification took several minutes of close observation. Nevertheless I had some success with Tph *Sc. iserti* during the latter seven months of the study. Iph fish were identified with the least success, except in the case of fish with very unusual markings (e.g. an Iph *Sc. iserti* at site B with a split tail; an Iph *Sc. taeniopterus* at site P with a "wavy" side stripe). The occupancies of those fish marked with acrylic paint are probably severely underestimated, for the paint faded in three to six weeks. The occupancies of Tph males who were present on the sites at the beginning or end of this study were also underestimated. Maximum observed occupancies probably give the best estimates for resident fish.

A. Description of behavioural categories

Residents

It became obvious early in the study that not all fish of the same species and phase behaved alike. Many were seen again and again in the same places. Such fish were classified as residents. They swam openly and were not chased out of their normal ranges by other fish.

Terminal phase residents were territorial as opposed to being simply site-attached [7] i.e. they defended the borders of their home ranges from other Tph males (see Figures 17 to 19, next chapter; Brown and Orians, 1970; Wilson, 1975). The territories of residents and home ranges of Iph fish often overlapped partially or entirely. When overlap was complete, the Iph residents were called a harem. The Iph fish residing within a harem were referred to as belonging to the Tph, and vice versa. Iph defended their ranges from like-sized individuals but did not exclude smaller fish. Well-developed territoriality in Iph female *Sc. iserti*, named yellowfins because of their bright yellow pelvic fins, was described in Panamianian populations (Buckman and Ogden, 1973; Robertson et al., 1976; Warner and Downs, 1977). I detected yellowfins at all sites (except site A where *Sc. iserti* was not abundant), but they were not as common or aggressive, nor were their pelvics as deep a yellow as those in Panama (pers. obs.). For the purposes of this discussion, the home ranges of Iph fish will not be termed territories although some defence of space may have occurred.

Transients and intruders

Another class of fish, non-residents or transients, behaved very differently, and were resighted only a few times at most. Transients moved in a directed manner over long stretches of the reef, stopping occasionally to feed. I did not count fish seen during sunrise or sunset migrations as transients (Dubin and Baker, 1981). Transients were sometimes chased or followed by resident fish. The transient Tph *Sc. taeniopterus* and *Sp. aurofrenatum* at site M behaved "nervously"; they would start and take cover if approached, and some were emaciated, in poor shape, with scales missing.

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[7] Site-attached implies remaining in the same area over some period of time (Sale, 1978c), but does not connote active defence of borders.

Intruder Tph males were a special category of transient fish, seen within the boundaries of another male's territory, often feeding quietly near coral heads. Tph *Sp. aurofrenatum* intruders behaved particularly surreptitiously, hanging beneath coral overhangs and moving very slowly. They also had a unique colour pattern, with a very dark red belly and dark orange-red, rather than yellow, post-opercular spots. They rapidly took on the normal male coloration when attempting to claim a vacated territory (see below). Tph *Sc. taeniopterus* intruders were less secretive and would feed calmly in the open, some turning an Iph-like striped pattern when a Tph male was nearby. Both *Sc. taeniopterus* and *Sp. aurofrenatum* intruders were viciously chased off when detected by a resident Tph. Intruders were harder to identify in *Sc. iserti*. They fed openly in territories and were often tolerated by resident males.

Known residents, "neighbours", also trespassed in other males' territories. However their behaviour was quite different from that of intruder transients. The neighbours generally swam openly, well above the coral, and were ignored, or escorted out at a distance of several metres by the resident Tph. Neighbours' "visits" were usually peaceable, but on several occasions Tph *Sp. aurofrenatum* crossed into a neighbour's territory, turning dark and mottled, and vigorously chased Iph fish.

Transient and intruder Tph were least common inshore at site M (Figure 14).[8] If the intrusion rate represents attractiveness of an area, sites A and B were most attractive to Tph *Sc. taeniopterus*, sites B and P to *Sp. aurofrenatum*. Tph neighbours trespassed most often at site P. I cannot adequately explain this phenomenon. One known neighbour shifted into site P from at least 50 m away. Site P's proximity to two reef slopes may have increased competition for territories there (see Chapter 8).

Some Iph fish were also transient. Transient Iph *Sc. iserti* and *Sc. taeniopterus*, were seen at all sites; they moved in groups, and fed often. They were occasionally chased by Tph males. The massive feeding aggregations of *Sc. taeniopterus* and *Sp. viride* that formed at site A (Plate 3; Chapter 4) were somewhat site-attached, moving over an area of at least 3000 m². On one occasion I found a second large feeding school of 100 Iph *Sc. iserti* and 50 Iph *Sc. taenioterus* ca. 300 m southeast of site A.

Transient Iph *Sp. aurofrenatum* were first noticed because of the unique instantaneous colour change and behaviour of Tph males who followed and inspected them. The males' normal green colour became mottled with white, the

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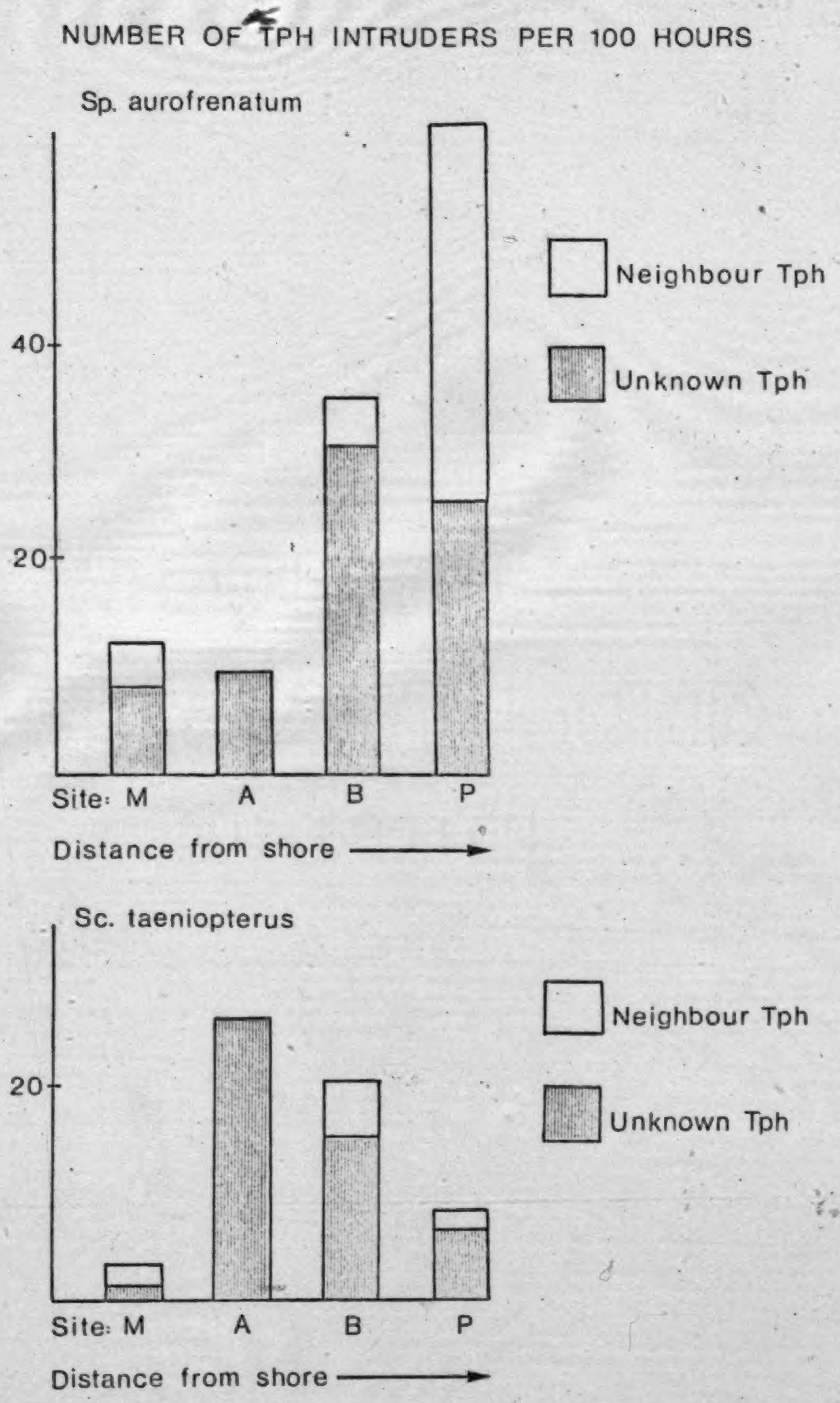
[8] I did not include any intruder Tph *Sp. aurofrenatum* seen during removal experiments at site B, and could not accurately detect Tph *Sc. iserti* intruders anywhere.

Figure 14. The number of Tph *Sp. aurofrenatum* and *Sc. taeniopterus* intruders seen at study areas over 1978-9. Neighbour Tph were known nearby residents while unknown Tph were transient intruders.



lower sides went deep red and a ventral white stripe, extending onto the tail, appeared. Typically, the male approached the one to three transient Iph and followed behind them in this unusual colour pattern with his snout held a few centimetres from the vent of one Iph. Following lasted for 10 to 30 seconds. The male then returned to his normal colour and would display to and chase the Iph fish. Tph *Sp. aurofrenatum* twice followed Iph *Sp. viride* and once several Iph *Sp. chrysopterum* in the same way. Iph residents also displayed to, followed and chased transients. Following occurred in 21 of 83 separate sightings of one or more transient Iph *Sp. aurofrenatum*, while chasing by either Iph or Tph residents occurred 34 times.

Transients were paler than residents, and had transparent, rather than red, anal and caudal fins and a metallic sheen to their bodies. They could rapidly revert to a normal colour. I speared five of these transient Iph. All were relatively large (SL 127-159 mm). One (SL 153 mm) was beginning to change sex but showed no signs of Tph coloration (see Reinboth, 1962, 1968 for histological criteria); its ovarian lumen was very large with only small, dark staining oocytes in the lamellae, a few atretic bodies, and proliferating spermatogenic cells. The other four had normal active female gonads, with large, yolky oocytes and empty follicles where eggs had been spawned.

Large, transient Iph *Sp. aurofrenatum* were also more common at the offshore sites than elsewhere (Table 17), and

Table 17. The number of transient Iph *Sp. aurofrenatum* seen at each study area over 1978-9, the number of observation hours at each site, and the number of transient Iph per 100 hours of observation.

Site	Number seen	Observation hours	Number per 100 hours
M	17	157.75	10.8
A	1	42.05	2.4
B	58	192.03	30.2
P	44	131.25	33.5

were seen at all times of the day. At site B they moved mainly northwest and southeast along the ridge top towards or away from the outer slope (Figure 2). I followed one fish for several hundred metres until it began to gradually descend the outer slope. They moved in all directions at site P, both towards and away from the north- and east-facing slopes. At site M they moved primarily inshore and offshore (east-west). Transients' status was unclear. The active state of their gonads, and their movements towards and away from reef slopes hints that they were migrating for spawning purposes. However, the existence of one sex reverser among them suggests that transitional *Sp. aurofrenatum* were also transients.

Residents may follow transient Iph's in order to determine their sexual status. Tph males would be especially likely to chase off Iph males which are potential mate competitors (Robertson and Warner, 1978). Tph *Thalassoma bifasciatum* also follow Iph males, inspect their anal region, and then chase them (Warner and Robertson, 1978). Randall and Randall (1963b) felt that Tph *Sp. rubripinne* detected Iph males by chemoreception. Aggression by Iph residents may also exclude potential mate competitors, i.e. other ripe females. Females of a temperate wrasse compete for early spawnings by chasing other females (Jones and Thompson, 1980). Female-female interactions require much more study in tropical labrids and scarids.

B. Duration of occupancy

Residents

The number of Iph fish identified (either by marking or by scar patterns) at each study area over the entire study is shown in Table 18. My success in identifying Iph fish was too low to compare the occupancies at different sites with much certainty. For *Sp. aurofrenatum* occupancies appeared similar. Despite intensive tagging, no Iph *Sc. taeniopterus* or *Sc. iserti* were seen beyond two to three months at site M. The Iph *Scarus* population there may have been more transient than at the other sites. Certainly some Iph *Scarus* resided permanently at sites B and P. One known Iph *Sc. iserti* was resident at site B for over a year before changing sex and remaining there. A *Sc. taeniopterus* at site P also remained after transforming to Tph colours. Assuming that the maximum durations in Table 18 are representative, Iph fish can be resident offshore for at least eight months.

The occupancies of Tph males were determined with more certainty (Tables 19 to 21). Maximum occupancies of Tph *Sp. aurofrenatum* and Tph *Sc. taeniopterus* were approximately two years. *Sc. iserti* remained at most eight months to one year. Since I knew the approximate number of territories in a site and could estimate when fish disappeared or entered the area from my weekly grid surveys, I could calculate the rate of Tph turnover in a territory over a year (Tph per territory per year). The inverse of this value (multiplied by 365) gives an estimate of the occupancy which is presented in

Table 18. Number of Iph parrotfish identified over the course of the study (1976-7 and 1978-9) at each site, and durations of occupancy (mean and maximum) in days.

	Site M	Site B	Site P
Sp. aurofrenatum:			
Number identified:	26	37	2
Mean occupancy:	23.2	19.3	75.0
Maximum occupancy	266	245	149
Sc. taeniopterus:			
Number identified	22	32	12
Mean occupancy	12.1	11.5	82.5
Maximum occupancy	68	125	286
Sc. iserti:			
Number identified	36	8	0
Mean occupancy	11.4	70.4	ND
Maximum occupancy	99	423	ND

Tables 19 to 21 as days per territory per Tph. The estimates agreed well with the observed occupancies except for *Sc. taeniopterus* at site P (Table 20), which had an extremely low changeover rate. However, the occupancies observed there were underestimates because most fish were resident throughout the entire study.

There was a marked difference between site M on the one hand, and sites B and P on the other in Tph *Sp. aurofrenatum* occupancies (Table 19). Territories at site M had a changeover rate of four to six fish per year, and the average occupancy of males was little over a month. At sites B and P, residents changed at a rate of 0.6 to 0.9 per territory per year, and males remained on average four to five months. Positional shifts were more common at site M as well.

Durations of occupancy were also slightly shorter and positional shifts more common in Tph *Sc. taeniopterus* at site M than for *Sp. aurofrenatum*, but the difference was less marked (Table 20). The changeover rate of *Sc. iserti* at site M was also somewhat higher than at sites B and P, although some residents were seen over a long period of time (Table 21). Resident *Sc. iserti* at site M were often missing, in spite of my careful searching for them. Information concerning their use of space (see next chapter) hints that they moved between scattered areas throughout the day, and perhaps migrated elsewhere to spawn.

The shorter occupancy times of Tph males at site M,

Table 19. Number of resident and transient or intruder Tph *Sp. aurofrenatum* identified in 1978-9 at each site, the number of territories overlapping each study area, the number of Tph residents entering, leaving or shifting position, and the turnover of Tph per territory per year. The mean and maximum observed occupancies are given in days, as are occupancies estimated from the turnover rate for residents.

	Site M ($3000\ m^2$)	Site B ($1800\ m^2$)	Site P ($1500\ m^2$)
Number of territories:			
Complete overlap[1]	4 - 7	4 - 6	5
Partial overlap[1]	2	2	2 - 3
Tph turnover:			
Positional shifts[2]	9	0	1
No of Tph disappearing	44	5	6
No. of newcomers	38	7	6
Tph/territory/year	3.9- 5.9	0.6- 0.9	0.6- 0.7
Days/territory/Tph	62 - 94	406 -568	497 -568
Residents:			
Duration (Days):			
Mean	37.6	143.6	166.6
Maximum	195	678	400
No. identified:			
Resident on site	50	22	13
Neighbours	13	20	20
Transients/Intruders:			
Duration (Days):			
Mean	1.0	3.3	20.4
Maximum	1	39	195
No. identified	3	44	23
Total Tph identified	66	86	56

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[1] Complete overlap: over 75% of territory within study area. Partial overlap: less than 75 %.

[2] Shifts included fish that completely switched position within the area, or moved gradually out of it.

Table 20. Number of resident and transient or intruder Tph *Sc. taeniopterus* identified in 1978-9 at each site, the number of territories overlapping each study area, the number of Tph residents entering, leaving or shifting position, and the turnover of Tph per territory per year. The mean and maximum observed occupancies are given in days, as are occupancies estimated from the turnover rate for residents.

	Site M ($3000 m^2$)	Site B ($1800 m^2$)	Site P ($1500 m^2$)
Number of territories:			
Complete overlap[1]	3 - 6	3 - 5	3 - 4
Partial overlap[1]	1	5 - 4.	2
Tph turnover:			
Positional shifts[2]	4	1	0
No of Tph disappearing	9	7	1
No. of newcomers	8	7	3
Tph/territory/year	1.0- 1.8	0.7- 0.8	0.3
Days/territory/Tph	200 - 351	487 - 568	1065 -1278
Residents:			
Duration (Days):			
Mean	137.8	298.3	200.8
Maximum	390	721	407
No. identified:			
Resident on site	14	14	5
Neighbours	7	3	7
Transients/Intruders:			
Duration (Days):			
Mean	1.0	38.5	1.0
Maximum	1	354	1
No. identified	7	19	8
Total Tph identified	28	36	20

---

[1] Complete overlap: over 75% of territory within study area. Partial overlap: less than 75%.

[2] Shifts included fish that completely switched position within the area, or moved gradually out of it.

Table 21. Number of resident and transient or intruder Tph *Sc. iserti* identified over seven months at each site, the number of territories overlapping each study area, the number of Tph residents entering, leaving or shifting position, and the turnover of Tph per territory per year. The mean and maximum observed occupancies are given in days, as are occupancies estimated from the turnover rate for residents. Only a portion of each site was observed.

	Site M ($3000\ m^2$)	Site B ($1800\ m^2$)	Site P ($1500\ m^2$)
Number of territories:			
Complete overlap[1]	2 - 3	5 - 7	7 - 8
Partial overlap[1]	2 - 4	2	1
Tph turnover:			
Positional shifts[2]	0	0	1
No of Tph disappearing	6	6	6
No. of newcomers	7	5	6
Tph/territory/year	1.6- 2.8	1.3	1.3
Days/territory/Tph	131 -229	271	284
Residents:			
Duration (Days):			
Mean	109.5	124.1	60.9
Maximum	343	278	280
No. identified:			
Resident on site	9	11	14
Neighbours	1	2	0
Transients/Intruders:			
Duration (Days):			
Mean	1.0	2.3	3.3
Maximum	1	9	10
No. identified	4	6	4
Total Tph identified	14	19	18

---

[1] Complete overlap: over 75% of territory within study area. Partial overlap: less than 75 %.

[2] Shifts included fish that completely switched position within the area, or moved gradually out of it.

particularly *Sp. aurofrenatum*, were probably not a result of higher mortality there since Iph *Sp. aurofrenatum* did not show the same trend. Piscivores were not noticeably more common at site M than elsewhere (Table 3), and those present were too small to handle mature parrotfish. Fishing pressure was also no more intense at site M, especially in 1978-9 when local fishermen agreed to stay away.

These temporary Tph *Sp. aurofrenatum* were not distributed evenly over site M. Eight males that lived during 1978-9 on the offshore-facing slope (primarily in the pillar coral zone; see Figure 3) had occupancies averaging 86 days. Seven males seen over the finger coral and other (mainly rubble) zone remained on average 24 days. Twenty-two males living over the middle of the area, primarily in the staghorn coral zone, remained for 46 days on average. The 29 Tph males seen in the shallow, inshore rubble and small coral zone were resident on average only 18 days. These differences were significant (Anova, $F(3,62) = 6.2$, $P < 0.001$). Thus the staghorn and shallow rubble zones had the most turnover, while the longest occupancies on average were for fish on the offshore-facing slope. Three of the nine positional shifts were for fish in this zone; two fish gradually shifted offshore and were lost from the record, while one moved northwest off the area. One fish from the finger coral zone shifted northwest. The others shifted within and between the staghorn and shallow rubble zones. No shifts occurred in an inshore direction. Jones (in press) found that male *Pseudolabrus celidotus* in shallower inshore regions had shorter occupancies than those in deeper offshore areas, and that space inshore was not immediately refilled as it was offshore. He also observed shifts in offshore directions from the temporarily inhabited areas, and related them to competition among males for good spawning sites in deeper water.

There was no such difference between zones in occupancies for Tph *Sc. taeniopterus* at site M (F(3,24) = 0.9, ns). Males occupied all portions of the site equally often. Three fish shifted south off the area, one moved north. My information on *Sc. iserti* was incomplete as I only observed them in the shallow inshore half of site M. I recorded both short-term and long-term occupancies for Tph *Sc. iserti* in the same zones of site M.

There were no changeovers of Tph *Sp. aurofrenatum* or *Sc. taeniopterus* over the two month observation period at site A.

My results show that most Tph, with the exception of Tph *Sp. aurofrenatum* and some Tph of the other species at site M, are long-term residents, remaining in their territories for over two years in some cases. *Sc. iserti* has a more rapid rate of turnover; the other species may live longer.

Intruders and turnover of individuals

Replacements of Tph residents by intruder Tph were investigated. Intruders, except those that became residents, were never seen more than five times (Tables 19 to 21). None at site M were seen more than once. At sites B and P, intruder Tph were seen occasionally in different parts of the study grid, often many days apart. Two site B Tph *Sp. aurofrenatum* that had first been identified as intruders later took over vacated territories. One male (#31) was seen behaving as a typical intruder on December 18, 1978 and January 2, 1979, before it was noticed on January 23 defending a territory (see Figure 17). The other was first noted on July 22, 1977 trespassing on the southwest corner of site B. Between August 3 and 5, 1977, this fish made an unsuccessful bid to claim a territory in the southeast corner where the resident seemed ill; he was covered in brown spots and only weakly attempted to repel the intruder. By August 9, the intruder was established in the northeast corner of the grid where another resident had perished in a fish trap.

These anecdotal observations reveal an intense struggle for vacated territories at the offshore sites B and P. When a Tph *Sc. iserti*, *Sc. taeniopterus* or *Sp. aurofrenatum* disappeared, his place was taken almost immediately by a Tph who came from a pool of wandering intruders. Shifts by known residents into vacated space were very rare (Tables 19 to 21).

In an attempt to determine the amount of time before an intruder male entered a vacated territory, I removed (either by spearing or confinement in traps) six Tph *Sp.*

aurofrenatum at different times and from different territories at site B.[9] The average time that elapsed until an intruder entered and began to defend the territory was 25.2 minutes (range 3 to 77 minutes). In nine other removals when my dive terminated before an intruder had arrived, there was an intruder present at the next dive, and the elapsed time averaged 5.4 hours. One exception occurred on Feb. 22, 1979 during a period of heavy swells. A resident was speared at 1100 hours. A neighbouring male swam and displayed in the vacated territory that day, but no intruder appeared. The seas were too high the next day for diving, but the following day a new resident was in place. Thus intruders may restrict their activity when conditions are disturbed.

As Thresher (1979a) described, removal of a resident Tph created a "power vacuum" in the empty space. Larson (1980c) noted a similar phenomenon in temperate marine rockfish. Often several intruders vied for control of the vacated territory. In four removal experiments where I could watch continuously for several hours, from one to four intruders made separate attempts to evict the new resident. Three of 8 attempts to displace newcomers were successful. The aggression levels during these struggles between intruder males were extraordinarily high, and fights could last for up to 20 minutes. Interactions between established residents generally endured only a few minutes at most. Such increased aggression when territories are being established occurs in other vertebrates (Morse, 1980).

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[9] Removal dates: Oct. 5, 1978; Oct. 9, 1978; Jan. 24, 1979; March 8, 1979; May 5, 1979; and May 17, 1979.

Although removal experiments were not performed on the other species, the situation was similar. Very little space went unclaimed at any of the offshore sites A, B and P (see Figures 17 to 19, Table 24), and no territories remained empty for any noticeable period. Tph *Sc. iserti* in Panama were replaced within two days (Robertson et al., 1976). Tph *Pseudolabrus celidotus* in New Zealand were also rapidly replaced by nonterritorial wandering males (Jones, in press).

At site M, vacated space was not immediately filled, although two days before several Tph males spawned there, one lost his territory to another after a protracted battle. On four occasions at site M, I confined Tph *Sp. aurofrenatum* in traps for 45 minutes to 24 hours. No intruders appeared. Territories of all three species at site M often went empty for several months, and the patterns of space use changed from sample to sample (see Figures 17 to 19). At sites B and P, a disappearance was generally balanced by one newcomer. Occasionally (e.g. *Sp. aurofrenatum* #1 at site B, Figure 17), an unusually large territory was refilled by more than one male, or a resident lost part of his territory to a newcomer but remained on site (e.g. Tph *Sp. aurofrenatum* #9, or Tph *Sc. taeniopterus* #4, both at site P, Appendix 2). This nearly one-to-one replacement of Tph males did not occur at site M, and the number of territories in use at any time varied more (Tables 19 to 21).

The reasons for disappearances of Tph males were usually unknown although some were fished in 1976-7. I watched two Tph *Sp. aurofrenatum* (#20 at site P and #1 at site B), and two Tph *Sc. taeniopterus* (#5 and #6 at site B), go into a physical decline and lose their territories. The territory of site B *Sp. aurofrenatum* #1 shrank from 580 m^2 (n = 3 samples) in June, to 544 m^2 in October (n = 2), and 371 m^2 (n = 1) in December due to neighbours' expansions (Figure 17, Appendix 2). On Dec. 16, 1978, this fish was observed, swimming very slowly and scarcely feeding. By Dec. 26, 1978, he had been replaced. A similar sequence occurred for site P Tph #20. On Dec. 1, 1978 he was seen hiding in his former territory while an unknown male displayed and attacked him. On Dec. 7, 1978, he was last seen, very emaciated with his post-opercular spots bitten and bruised.

The two Tph *Sc. taeniopterus* also appeared tattered and thin before their disappearances. Tph #6 reappeared once six weeks later as an intruder in another part of site B, emaciated and with dark spots, perhaps parasites, on his scales. I occasionally saw sick-looking Tph *Sc. iserti* as well.

In summary, Tph males that disappeared from sites B and P were rapidly replaced by intruder Tph. Occasionally neighbours expanded their territories to claim parts of a vacated one. Unlike redlip blennies (Nursall, 1977) and rockfish (Larson, 1980c), neighbouring residents completely filled emptied territories only rarely. Territories were not rapidly refilled at site M. Tph residents may have lost their territories due to disease or senility, but territory loss did not always result in immediate death of the fish.

C. Fish sizes

Parrotfish varied more in size at site M than elsewhere (Table 22). Visual estimates were not used in Table 22, but agreed well with the actual measurements. Iph *Sp. aurofrenatum* at site M were smaller than fish at the other sites (t-tests). The average size of Tph *Sp. aurofrenatum* was also lower at site M, and greater at site A than elsewhere. Iph *Sc. taeniopterus* were largest at site P. There were no differences for any of the other groups.

The frequency distribution of *Sp. aurofrenatum* sizes at sites M and B, where sample sizes were largest, is shown in Figure 15. Tph *Sp. aurofrenatum* size varied more at site M than at site B. Some very tiny males associated with much larger Iph fish at site M, in contrast to Robertson and Warner's (1978) statement that they should overlap only a few millimetres in size at any locale. The size classes of Tph males at site M did not segregate into different substrate zones.

The size range of Tph males was surprisingly small at site B, the great majority of males being between 150 and 165 mm SL. My visual estimates at site P gave the same narrow range. At site A, collections and visual estimates

Table 22. Mean sizes of fish measured in 1976-7 and 1978-9 at each site. Standard length in mm, range, n = sample size. Only actual measurements, not visual estimates are given.

	Site M[1]	Site A[2]	Site B[1]	Site P[2]
Iph *Sp. aurofrenatum*	121.1 66-155 n=31	138.7 94-160 n=11	133.1 92-153 n=51	139.6 115-165 n= 8
Tph *Sp. aurofrenatum*	144.9 115-190 n=44	172.4 140-200 n=10	157.7 130-176 n=55	155 n= 1
Iph *Sc. taeniopterus*	134.1 63-180 n=44	140.6 112-164 n= 5	127.4 83-148 n= 8	158.9 142-181 n= 7
Tph *Sc. taeniopterus*	199.6 161-240 n=16	194.4 176-208 n=13	190.0 176-220 n= 8	186.3 175-206 n= 7
Iph *Sc. iserti*	96.5 44- 80 n=126	ND	99.0 80-118 n= 2	ND
Tph *Sc. iserti*	149.6 123-180 n= 6	140.3 136-145 n= 3	140.3 137-145 n= 3	ND

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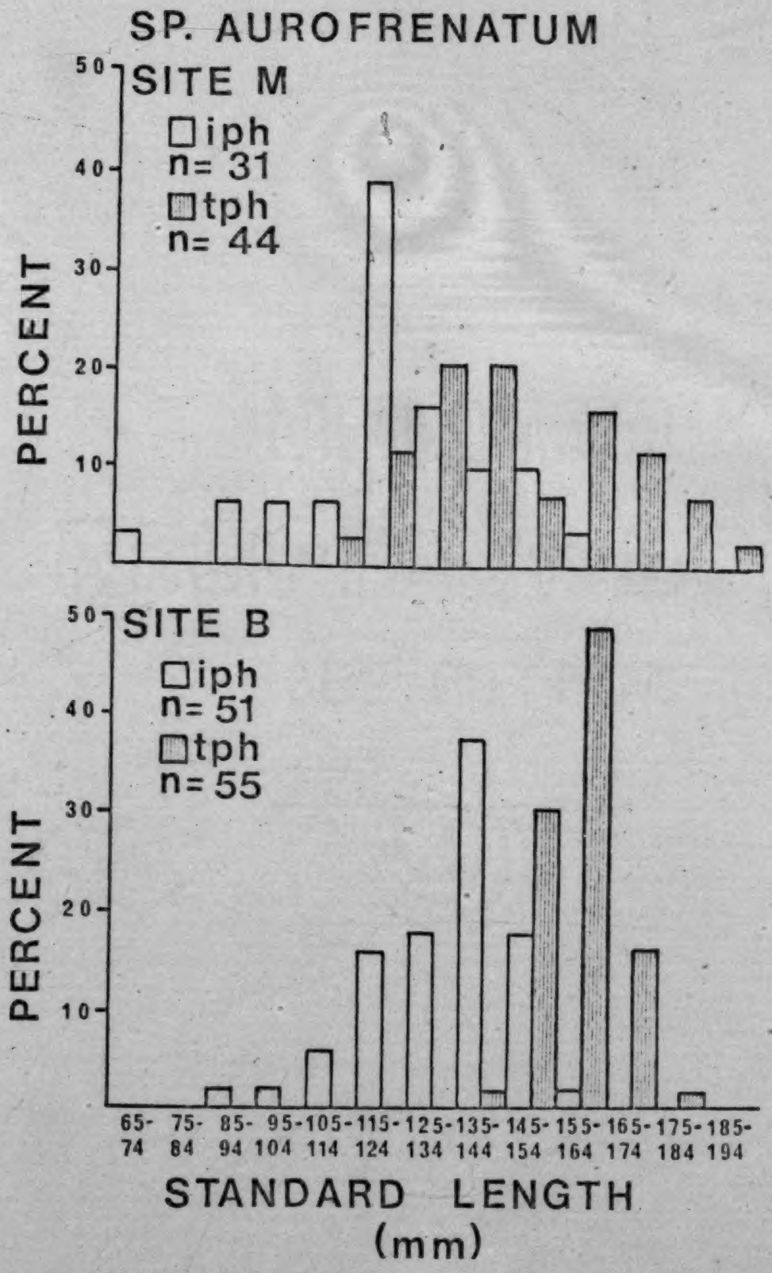
[1] Measurements of live-trapped and released fish, or of fish collected in areas near sites M or B.

[2] Collections made in 1976-7.

Figure 15. Frequency distribution of *Sp. aurofrenatum* size classes at sites M and B. Only actual measurements, and not visual estimates were used.



found more fish at the larger end of the spectrum, with the range nearly as narrow as at sites B and P. The status of a Tph male at site B (i.e. resident, or transient/intruder) was independent of its size class[10] ($X^2(2) = 2.65$, ns). In other words, intruder and resident Tph at site B did not differ in size. This was also true at the other sites. Jones (in press) also found that residents and intruders of *Pseudolabrus celidotus* were the same size. Clavijo (1980b, and pers. comm) did find that intruding Tph *Sp. aurofrenatum* diminished progressively in size after she repeatedly removed all males from a 1350 m² area in Puerto Rico. While some intruders there were smaller than the average resident, these fish were not the first to turn up in a vacated territory.

At site M, Tph *Sc. taeniopterus* also ranged more widely in size when compared to the barrier reef sites (Figure 16). Too few intruder males were seen to test whether they differed in size from the residents, but my impressions were that they did not.

My data for *Sc. iserti* are sparse, but this species also appeared to vary more in size at site M (Table 22). Warner and Downs (1977) found that territorial males were larger than transient Tph *Sc. iserti*, and their length increased with depth.

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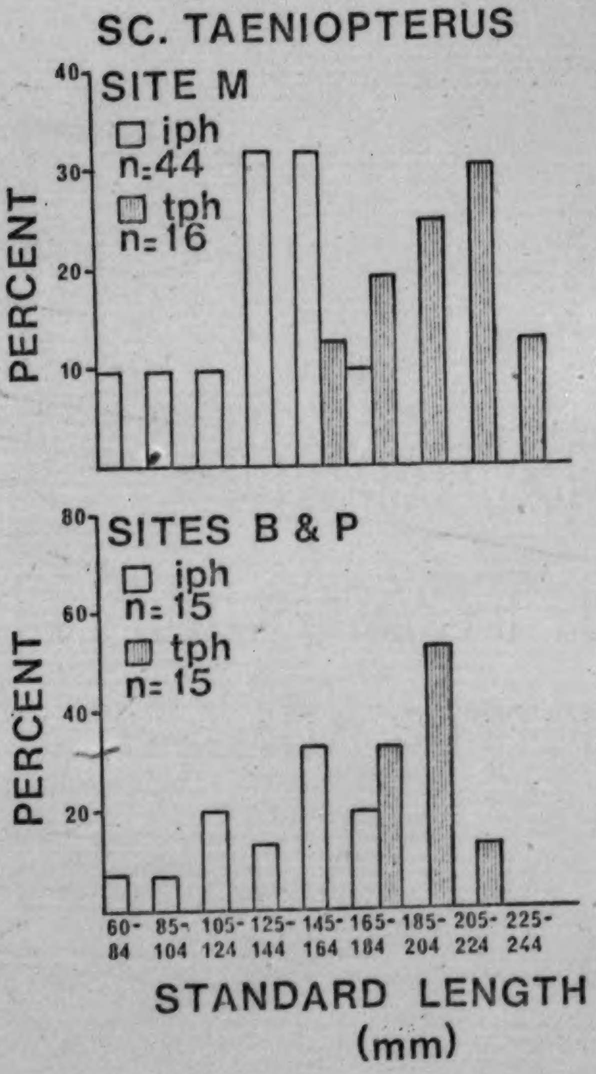
[10] size classes: small < 150 mm SL, medium < 165 mm SL, large > 165 mm SL.

Figure 16. Frequency distribution of *Sc. taeniopterus* size classes at sites M, B, and P. Only actual measurements, and not visual estimates were used.



D. Sex reversal

The control of sex reversal in scarids is poorly understood. *Sp. aurofrenatum* is monandric (Robertson and Warner, 1978), and therefore all transitional fish were sex reversers. Transitional fish were identified as having elements of both Iph and Tph colours. The *Scarus* species studied are diandric. Primary males make up 25 % of *Sc. iserti* populations (Warner and Downs, 1977; Robertson and Warner, 1978) but only 8 % of *Sc. taeniopterus* (Dubin, 1981). Thus transitional *Scarus* could be either sex reversers, or Iph males changing into Tph colours.

I looked for transitional fish at all study areas in order to determine whether reversal or phase change

1. occurred seasonally,
2. was more common at some sites than at others,
3. followed Tph male disappearance.

I was able to determine a rough sequence of Tph colour pattern development by watching known individuals reverse over a period of several days. In *Sc. iserti* and *Sc. taeniopterus* Tph colours first developed on the snout, and the edges of the dorsal, anal and caudal fins (see Plates 2 to 6; Bohlke and Chaplin, 1968; Randall, 1968; or Chaplin and Scott, 1972 for colour patterns).

The transitional pattern of *Sc. iserti* has been described (Randall and Randall, 1963b; Buckman and Ogden, 1973). Transitional *Sc. iserti* moved with groups of Iph fish, some of which engaged in group spawning (see also

Randall and Randall, 1963b). They were least common at site B, perhaps because neither loose feeding associations like those at site M, nor large group spawning aggregations like those at site P (Chapter 7) appeared there (Table 23).

In two days, a *Sc. taeniopterus* at site B transformed from a clearly recognizable Iph fish with Tph colours just barely visible on the snout, to a pale Tph. Tph colours developed last on the sides, which were pale yellow below and brown above. They remained faint for some time; a site P *Sc. taeniopterus* transformed at the end of April, 1979, but in July was still less bright than other Tph males. Transitional *Sc. taeniopterus* fed and swam openly, but took on an Iph-like striped pattern and arched submissively when a Tph approached. Several were seen amidst the large feeding school of mostly Iph fish at site A.

Transitional *Sp. aurofrenatum* were solitary and secretive. Their transformation was rapidly completed. After a three week series of male removals, an acrylic-marked Iph fish at site B developed Tph colours between August 1 and August 4, 1977. On August 1, I noticed that its normally dark Iph eyes were reddish, and it had developed the pink Tph stripes at the corner of the mouth. It was ignored by passing Tph, and displayed weakly to other Iph. By the next day black tips appeared on its more and more lunate tail. That morning the black post-opercular spot appeared as a faint smudge. It was clearly visible by afternoon. The transitional fish chased other Iph, and displayed to a resident male in a long encounter that included one mouth-to-mouth contact. By August 4, this fish had all the Tph colours except the yellow post-opercular spot which develops last. It behaved very secretively, hugging close to coral overhangs in its habitual range. At one point it fed with the resident Tph, arched submissively to it (see Chapter 7), and displayed to Iph fish. The next day it had disappeared, perhaps chased away by the resident Tph. The fact that Iph fish were collected with transitional gonads indicates that sex change precedes colour change.

Transitionals were seen throughout the year. Nine of 27 transitional *Sp. aurofrenatum* (33 %), and ten of 23 *Sc. taeniopterus* (43 %) were seen in March-April, 1979. However the data are insufficient to determine whether sex change occurs on a seasonal basis, as in some temperate hermaphrodites (Warner, 1975a; Dipper and Pullin, 1979; Jones, 1980).

I hypothesized that if sex reversal occurred as a result of male disappearance, as it does in several labrids (*Labroides dimidiatus*: Robertson, 1972, 1973; *Thalassoma bifasciatum*: Warner et al., 1975, Warner and Hoffman, 1980a; *Bodianus rufus*: S.G. Hoffman, pers. comm.) and the serranid *Anthias squamipinnis* (Fishelson, 1970; Shapiro, 1977, 1980, 1981), then transitional *Sp. aurofrenatum* should be most common at site M where Tph turnover was highest. When numbers of transitionals were standardized to reflect the density of Iph populations, this was true (Table 23). Since most of them were in the first stages of colour change when sighted, and given the rapidity of the entire process, most transitionals probably arose from local Iph residents. *Sp. aurofrenatum* sex changers were more common at site B where removal experiments were made than at site P.

In August, 1979, I removed all Tph *Sp. aurofrenatum* from a patch reef in the San Blas Islands, Panama. After 17 days no transitional fish had appeared, although several Iph with pale tails, perhaps about to become transitional, were seen, and Iph moved more freely over the reef than they did on an unmanipulated one. I. E. Clavijo (pers. comm.) found no sex reversal after mass removals of Tph *Sp. aurofrenatum* in Puerto Rico, although Iph fish deserted the area. I noted the same phenomenon in August, 1977, after a three-week series of male removals at site B. The transient Iph described above contained some sex transformers. Large Iph females may leave their home ranges when Tph males are absent, and transform into males later.

In *Sc. taeniopterus*, there is some evidence for social control of sex reversal. Transitionals were most common at site M where there was unclaimed space. Nineteen days after a Tph *Sc. taeniopterus* disappeared at site B (#4, Figure 18), two fish in the process of changing from Iph to Tph colours (#13, #14) were seen in his former territory. Parts of his territory had already been claimed by other fish (#12, #17). Both transitionals were present until early May when one disappeared (#14). He returned a week later and

Table 23. Number of transitional (i.e. changing from Iph to Tph colours) fish seen at each study area during 1978-9, and number per Iph fish per 1000 hours of observation.

	Site M	Site B	Site P
Sc. iserti:			
Number	8	5	7
Number/Iph/1000 hours	0.73	0.61	0.88
Sc. taeniopterus:			
Number	10	9	4
Number/Iph/1000 hours	4.3	2.3	3.3
Sp. aurofrenatum:			
Number	9	11	7
Number/Iph/1000 hours	7.0	6.5	3.6

reestablished himself. The other new Tph disappeared in early June and was quickly replaced by an intruder male. Eight of the other transitional *Sc. taeniopterus* (35 %) were seen in areas that had been empty for some time (at site M) or from which a Tph had retracted his territory.

Fish transforming within other males' territories were seen in all three species, and have been reported for *Sc. iserti* in Panama (Buckman and Ogden, 1973). One known Iph *Sc. iserti* transformed and remained in the same place at site B. Transformation in this species takes 10 days (Robertson and Warner, 1978).

Sex and phase change in the three parrotfish species observed here is not tightly controlled by social factors. It occurs over a wider size range in *Sp. aurofrenatum* than in the *Scarus* species, as Robertson and Warner (1978) reported (compare Figures 15 and 16). The transitional *Sp. aurofrenatum* measured or collected ranged in size from 115 to 153 mm SL (n = 9). *Sc. taeniopterus* transitionals measured 150 to 170 mm SL (n = 5). The one transitional *Sc. iserti* measured was 104.5 mm SL, in agreement with Warner and Downs' (1977) transformation range of 95 to 105 mm.

Age or size may determine when protogynous hermaphrodites transform (Warner, 1975a, 1975b; Warner and Downs, 1977; Jones, 1980). The *Scarus* species may change sex over a narrower size range than *Sp. aurofrenatum*. However, Bruce (1980) reported dwarf sexually active *Sc. psittacus* on the inshore grass flats at Aldabra Atoll. Clearly no single factor: sex, age, or social conditions, can explain the control of sex reversal in this diverse group of fish.

E. Summary and discussion

The population processes were different at site M than elsewhere, particularly for *Sp. aurofrenatum*. Despite stable adult population numbers (Table 7), Tph individuals turned over rapidly there. Iph and Tph *Sc. iserti* and *Sc. taeniopterus* remained only temporarily at site M, although some Tph remained for up to a year. There were fewer transient and intruder males at site M (Figure 14), and vacated Tph territories were not immediately refilled as at sites B and P. Shifting of position, both within and off the area occurred most often at site M. Although site A was monitored for only two months, the information available on space use patterns (see next chapter), and the lack of individual turnover in that time period, indicated that it resembled sites B and P, with permanent residents and many intruders. Competition for space among Tph males was greatest at the offshore sites. Clearly site M was not a preferred environment for Tph individuals, as it would have been if abundant food were a primary determinant of habitat quality (see Chapter 3).

The information on sizes also sets site M apart from the others. Iph and Tph fish all ranged into smaller size classes there (Table 22, Figures 15 and 16). Given that mortality rates did not differ among study sites, this could have been brought about in three ways:

1. Iph fish could have been deprived of food,
2. Iph fish could have been changing sex at smaller sizes,
3. Iph fish could have been deserting site M when they reached larger sizes.

Certain evidence makes the first possibility unlikely. Food, as measured on settlement plates, was more abundant at site M than elsewhere (Chapter 3). Also, growth rates of Tph *Sp. aurofrenatum* at site M were high. Three fish (one in each size class), remeasured after 35 to 82 days, had grown 5.87 mm per month on average (S.D. = 1.41). Randall (1961b) recorded growth rates of 3.5 to 20 mm per month in tagged adult parrotfish inhabiting sea grass beds in the Virgin Islands. At site B the growth rate of six Tph males remeasured after five to eight months was significantly lower, 0.69 mm per month (S.D. = 0.38; Mann-Whitney U test, $U = 0$, $P < 0.025$). Finally, the ovaries of many fish collected at site M had large yolk-filled oocytes (Warner, 1975a), which would not be expected in food-deprived fish (Bruce, 1980).

There were indications that site M Iph fish were transforming into Tph at smaller sizes (point two, above). Some Tph males were smaller in all three species at site M than elsewhere (Table 22, Figures 15 and 16). The smallest transitional *Sp. aurofrenatum* seen (ca. 110 mm SL) was at site M. More transitionals were seen there per capita in two species (Table 23).

It is likely that some Iph fish did leave site M. Recruitment of small Iph *Sc. taeniopterus* to site B has been described (Chapter 4). The lack of juvenile *Scarus* at sites B and P meant that Iph *Scarus* necessarily came from elsewhere. Transient Iph *Sp. aurofrenatum* were seen moving between the offshore barrier reef and site M, and *Sc. taeniopterus* regularly commuted between reefs (Dubin and Baker, 1981), so migrations of Iph from inshore to offshore areas were possible. Some of the large transient Iph *Sp. aurofrenatum*, and the wandering *Sc. iserti* and *Sc. taeniopterus* groups may have originated in inshore areas.

Tph males of all three species ranged more widely in size at site M than elsewhere. The smaller Tph probably eventually enlisted in the pool of transient intruders offshore. The larger Tph *Sp. aurofrenatum*, also temporary residents at site M, and often in poor physical condition, could have been fish who had lost their territories elsewhere. The same could be said for the larger *Sc. iserti* and *Sc. taeniopterus*, although some of these were long-term residents.

A synthesis of this information allows construction of a hypothetical life history sequence for these species. *Scarus* juveniles recruit primarily to inshore areas (Chapter 4), and eventually migrate offshore to join large feeding aggregations or loose wandering associations. Iph females may join harems, Iph males probably do not. After sex and/or colour change, a Tph male may "inherit" part of his former range, or become an intruder until a space becomes available. Having acquired a territory, the Tph male remains there until he dies, is driven off into inshore areas, or is forced to become an intruder once again.

The situation for *Sp. aurofrenatum* is similar. Juveniles recruit at all sites, and may stay on at maturity. Offshore populations may be augmented by the arrival of Iph adults from inshore. Large Iph in the process of sexual transformation, and other females migrating for spawning purposes become transients. Other Iph may transform within their home ranges, to become intruder Tph. At the loss of a Tph resident, some Iph's may desert and become transients while an intruder Tph rapidly takes the former male's place. Clavijo (1980b) suggested a similar sequence for *Sp. aurofrenatum* in Puerto Rico. Males who lose their territories, along with those too small to compete successfully for one, end up in less preferred inshore areas. Most males remain there only temporarily before joining or rejoining the queue of intruders offshore.

In summary, competition for space at the offshore sites is heavy, and fish that obtain space there remain relatively permanently. A population of "surplus" intruder males exists, prepared to take over vacated space immediately. In *Sc. taeniopterus*, intruders are most abundant at sites A and B; in *Sp. aurofrenatum*, at sites B and P. Transient Iph fish are also more common at the offshore sites. Their status as ripe females or sex reversers, requires further investigation. The factors controlling sex reversal remain to be clarified, although a social component may act in some species. Size alone does not account for sex reversal in *Sp. aurofrenatum*.

The life history of parrotfish is complicated not only by protogynous hermaphroditism and dual male origins, but also by the existence of several behavioural categories within each sexual type. Only continued detailed behavioural studies, combined with extensive collection and improved aging techniques (e.g. Thompson and Contin, 1980), will add more details to the life history sequence proposed here.

VII. Parrotfish social behaviour: use of space and time

Analysis of a species' use of space allows characterization of its social system. When spatial utilization patterns are compared over a range of habitat types, it is possible to determine what ecological factors affect them. Likewise, the way an animal allocates its time to different activities can illuminate both the animal's priorities (e.g. feeding, reproducing), and its behavioural responses to varying environmental conditions. Interactions are of particular interest because they are responsible for maintenance of social structures. When information of this sort is gathered for several cohabiting species, their adaptations for sharing resources such as space and food can be uncovered.

A. Behavioural repertoire

A brief description of the behavioural repertoire of parrotfish is presented here, with differences between species noted. I distinguished seven major categories of behaviour.

Swimming

Parrotfish normally swam by flapping their pectoral fins. Swimming could have had numerous functions such as foraging, patrolling, or displaying the fish's presence, but these were indecipherable because the movement pattern was identical in each case. I distinguished high swimming, i.e. moving through the water at least 2 m from the tops of the coral, from the more common low swimming. Tph males, when high swimming, would progress very slowly, alternating fin flaps with gliding. High swimming *Sc. taeniopterus* often developed delicate mauve margins on their lateral scales. Both Iph and Tph occasionally swam high in the water when feeding on plankton or suspended matter (Barlow, 1975; Robertson et al., 1976)

During aggressive encounters, and occasionally when startled, fish swam rapidly by flexing the tail. I counted such rapid swimming as aggressive behaviour (see below) when it occurred during an interaction, but if I was unable to locate a partner, I classed it as miscellaneous behaviour.

Feeding

When feeding, *Sp. aurofrenatum* oriented its head toward the substrate, stopped moving several cm from the object, and then moved forward and grasped or grazed it with a powerful bite, often twisting its body. The fish would bite, withdraw, bite again and so on. I did not count foraging, i.e. swimming from one food source to the next as feeding. Both Iph and Tph *Sp. aurofrenatum* could take on a striped pattern when feeding or stressed (Barlow, 1975). *Scarus* species oriented head-down when grazing on horizontal objects, and head-up on vertical ones. They did not move back and forth, and kept their mouths close to the substrate while gently scraping it in rapid bursts. Detailed analyses of feeding were made separately from activity budget measurements as described in Chapter 2.

Sitting

Any time the fish did not move forward, was in view, and was not being cleaned (see below) or interacting with another fish, its behaviour was classed as sitting. Fish sat suspended in the water or leaned against objects on the bottom. *Sp. aurofrenatum* often sat motionless in between the back and forth feeding bouts described above, particularly when feeding amidst staghorn coral thickets. Parrotfish did not often sit among gorgonian fronds, which they apparently do elsewhere (Barlow, 1975; Thresher, 1977b).

Interacting with damselfish

Parrotfish were attacked by damselfish, primarily *E. planifrons*, when swimming by one's territory, feeding within it, or approaching it head down in a feeding position. The damselfish would advance upon and sometimes nip the parrotfish, which would twist or dart away quickly, or back off slowly.

Miscellaneous behaviour

A number of activities occurred too rarely to be analysed separately, although I recorded them in detail during sampling. These included:

1. Extending the median fins; fin erection was part of aggressive interactions, but was classed as miscellaneous behaviour when no other fish was in sight and when it did not precede or follow other aggressive behaviour (see below).
2. Twitching the body; this often occurred as the fish

swam. Occasionally fish would shiver. Randall and Randall (1963) reported similar behaviour in sexually active Iph male *Sp. rubripinne*.

3. Rubbing against objects; all parrotfish occasionally veered towards benthic objects and rubbed their heads or sides against them in passing. Before sunset, *Sc. taeniopterus* rubbed against the gorgorian, *Plexaura edwardsi*, perhaps in response to light-dependent activation of its mucous gland (Dubin and Baker, 1981).
4. Sitting under cover; this was most common in *Sp. aurofrenatum*, but all parrotfish occasionally moved under coral overhangs so that I could not always see what they did.
5. Cleaning; fish would swim up to a goby cleaning station and solicit by holding a horizontal, or head-up position with the fins extended and the mouth often open (see Plate 6; Eibl-Eibesfeldt, 1955; Feder, 1966; Losey, 1971). Others leaned against the coral head while a goby or shrimp scuttled over them. Sometimes *Sp. aurofrenatum* rolled completely over on its side as a shrimp cleaned it. The *Scarus* species rested on their bellies during cleaning by shrimp. Rarely fish would start violently, dart away, or chase some small fish while at a goby station. They had perhaps been attacked by the wrasse blenny, *Hemiemblemaria simulus*, a cleaner-fish mimic (Randall and Randall, 1960).
6. Rapid swimming; as described above.

7. Unknown, or out of sight; this occurred when a fish was momentarily lost from sight during behaviour recording and I could not locate it.

Interactions

Interactions were classed as submissive or aggressive. Submission occurred rarely but was relatively stereotyped among the different species. A subordinate fish compressed its median fins, arched sideways with its body concave to the dominant fish, and stiffly swam off parallel to the other. Sometimes a fish arched with its body directly across the path of the dominant (see Plate 5). Yellowfin Iph *Sc. iserti* "greeted" (Buckman and Ogden, 1973) their Tph in the early morning by arching repeatedly in front of them with their pelvic fins extended. Most dominant fish appeared to ignore the arching fish.

Aggression varied in intensity. Low intensity interactions included supplanting and following behind another fish. Tph or large Iph performed these towards smaller Iph. Following of transient Iph *Sp. aurofrenatum* by Iph and Tph residents was described in Chapter 6. One fish swimming or feeding near another would occasionally turn towards and rapidly approach the other. I called this nipping, although actual contact rarely occurred because the second fish invariably moved out of the way. Nipping occurred over short distances and resulted in only minor displacement of the receiver, so it was considered a low level aggressive activity. Tph of all three species would tilt to one side and approach an Iph fish which would move aside. Tilting appeared to be a low intensity intention movement, as were weak displays, i.e. partly extending the median fins. Finally, if a fish was arched to by another, I considered that the first had performed a low intensity aggressive activity.

High aggression activities included fin erection and tailstands (Winn and Bardach, 1960; Randall and Randall, 1963; Barlow, 1975), chasing, parallel swimming and mouth to mouth contact or displays. The simplest interactions consisted of a Tph fish rapidly chasing an intruder out of his territory (Plate 2). Chases that occurred along territory boundaries often brought the neighbour Tph over to join in, and the intruder was expelled over a long distance. The fleeing fish swam with his median fins compressed. Interactions of longer duration included erection of the median fins and tilting upwards in a tailstand (see Plate 5). *Sp. aurofrenatum* occasionally leaned on the bottom while tailstanding. Two fish would tailstand side by side, alternately erecting their fins and turning to bite the bottom violently. Tph *Sc. taeniopterus'* upper sides turned a dark purple, and their side patch an intense yellow during aggressive displays. The yellow head patch of Tph *Sc. iserti* also intensified (Barlow, 1975). In parallel swimming two fish swam back and forth, side by side along a territory boundary. Mouth to mouth displays occurred when two fish faced each other and opened their mouths. These were seen very rarely in *Sc. taeniopterus* and *Sc. iserti* but occasionally in *Sparisoma*. Intruder Tph *Sp. aurofrenatum* fighting over a vacated territory would grapple with their mouths and both push forward, rise in the water 3 to 4 m, release each other, swim rapidly to the bottom and grapple again. I never saw such intense aggression between established residents.

All of these behaviours were performed by Iph fish as well. The aggressive behaviour of yellowfin Iph has been described (Buckman and Ogden, 1973; Robertson et al., 1976). These could vary the intensity of the yellow pelvic fins and possessed two lines of brown "stitching" along the belly which could also fade or darken.

Tailstanding was not invariably an aggressive display; fish in feeding aggregations (*Sp. viride, Sc. iserti, Sc. taeniopterus*) would tailstand before moving on. Parrotfish all did this at sunset, perhaps to enhance their visual fields or measure changing light levels (Dubin and Baker, 1981). I did not see any such tailstands during normal activity budget sampling.

Tph *Sp. aurofrenatum* performed a unique display which I called swooping, when a neighbouring male violated their borders.and did not retreat when the resident approached. Two broad red stripes appeared on the resident's body, one along the midline, the other on the belly, and he swam rapidly back and forth before the intruder in a sinusoidal manner, median fins compressed. This display was particularly common in newly arrived Tph. In the same situation, *Sc. taeniopterus*, would blanch along the dorsal fin and midline before attacking.

Reproduction

Courting and spawning have been well described in these species (Winn and Bardach, 1960; Randall and Randall, 1963; Buckman and Ogden, 1973; Barlow, 1975; Warner and Downs, 1977; Robertson and Warner, 1978; Dubin, 1981). Except in *Sc. iserti*, it normally occurred outside the time period of activity budget sampling. *Sp. aurofrenatum* spawned late in the afternoon, *Sc. iserti* around mid-day, and *Sc. taeniopterus*, early in the morning (see Table 33). Courting Tph males coursed rapidly around their territories using pectoral fin flaps, with the tail and median fins compressed. Bob-swimming (Barlow, 1975) was common. Tph *Sp. aurofrenatum* showed dark smudges behind the eyes when courting. Female parrotfish "solicited" (Thresher, 1979a) by hovering several m from the bottom, and the male approached and "quivered" above them (Robertson and Hoffman, 1977). Pair spawning consisted of a rapid dart upwards, release of gametes at the apex, and a rapid return to the bottom. Predation on spawners or their eggs was not seen. Group spawning was observed only in *Sc. iserti*, and was typical of previous descriptions (Randall and Randall, 1963; Barlow, 1975; Colin, 1978).

Parrotfish lack parental care or social groups bonded by amicable interactions and as a result their behavioural repertoire is more limited than in other groups (e.g. Barlow, 1967; Myrberg, 1973; Keenleyside, 1979). However, my descriptions scarcely do credit to the multitude of rapid colour changes which parrotfish can produce. A rich field of enquiry exists in the interpretation of visual signals and communication on coral reefs.

B. Use of Space- overall patterns

In this section the overall patterns of space utilization are described with the aim of characterizing each species' social system, determining variations in the system from site to site, and the amount of interspecific exclusiveness in use of space. I will discuss three parameters of overall space utilization:

1. packing, the extent to which territories form a contiguous mosaic, or are isolated from others;
2. permanence, the consistency of boundaries from sample to sample over both short (24-72 hours) and long (6 months) periods of time;
3. exclusiveness, the amount of overlap between Iph and Tph conspecifics and between different species.

I will also discuss home range or territory size, and which factors (e.g. food supply, fish activity budget, size or duration of occupancy) might affect it.

In order to analyse space use patterns, I generated territory maps for each species, site and sampling period in the following way. A sampling period was the three to ten day (sometimes longer) interval over which all residents at a site were mapped. Samples consisted of the position and behaviour of a fish, marked down at five-second intervals (see Chapter 2). After each day's sampling, the boundary enclosing all the fish's positions was drawn by hand on a scale map of the study grid, and the locations of any interactions were noted. When samples were completed, the total territory was outlined by tracing the outermost perimeter of the composite samples (see Figure 17). Thus the perimeter drawn enclosed 100 % of the fish's positions, and the boundaries were exact. This method avoids arbitrary decisions to count certain locations as 'excursions', to exclude certain points based on the distance from a centre of activity, or to generate hypothetical boundaries based on minimum or convex polygons (e.g. Michener, 1979; Ewald et al., 1980; Larson 1980b). While such methods are valuable, they were inappropriate for parrotfish which were both continuously visible, and lacking any core or centre of activity (pg. 203).

In addition to the hand-drawn maps, I generated computer maps (Appendix 2, Figures 22, 23). Each 30 m^2 quadrat on my scale maps was divided into six 5 m^2 subquadrats, and the number of each behaviour occurring there during a particular sample was recorded. A composite map was produced on the computer by placing the individual's number in that position on the map. Overlaps appeared as numbers placed above or beside another on the page. I mapped positions based on presence alone (regardless of activity, Appendix 2), and also specific activities, e.g. aggressive interactions, as well. Computer maps were drawn only for the 1978-9 data, as the earlier samples had been coded differently. Neither hand-drawn nor computer-generated maps accounted for the percent of time spent in a quadrat. This is considered below.

Packing

The hand-drawn maps of Tph males' boundaries show clearly that I was dealing with territories, i.e. defended areas (Brown and Orians, 1970; Wilson, 1975). Aggressive interactions almost always took place near the limits of the fish's movements (*Sp. aurofrenatum*: Figure 17; *Sc. taeniopterus*: Figure 18; *Sc. iserti*: Figure 19, Table 29). Maps for site M and B only are shown. Computer maps for sites A and P, which resembled those at site B, are found in Appendix 2. Since territoriality was not clear-cut in Iph fish, their areas are termed home ranges for the purposes of this discussion.

There were clear differences in packing between site M on the one hand, and sites A, B and P on the other. Tph males at site M showed much looser packing of space than elsewhere. At the offshore sites contiguous territories formed a mosaic; inshore, large amounts of space went empty and some territories were isolated. I estimated the amount of packing by Tph males on computer maps by counting the number of subquadrats used by one or more fish, and expressing these as a percentage of the total subquadrats in a study area (Table 24). Tph males of all three species used less than 60% of the available space at site M. Elsewhere 80% or more was claimed. These differences were not due to differing amounts of observation time at the sites- each individual was observed on two (sometimes one or three occasions) and for approximately the same amount of time at all sites.

Sites with the highest intrusion rates (Figure 14) had the tighest packing: site A for *Sc. taeniopterus*, site P for *Sp. aurofrenatum*. Although *Sc. iserti* intruders were not measured, group spawning (and thus probably intruders, see Warner and Hoffman, 1980b) was most common at site P where packing was tightest. High intrusion rates might cause contraction of territory boundaries and thus closer packing (Myers et al., 1979) but the relation is not a simple one. Both tightly packed territories and high intrusion rates may result from residents' and intruders' attraction to areas of good quality (e.g. Ewald et al., 1980). Synchronous arrival could cause tighter territory packing (Knapton and Krebs, 1974), but this was unlikely to have occurred at any of the sites. My weekly surveys showed that individuals disappeared and were replaced one at a time, and even local fishing patterns were not intensive enough to denude a 1500 m^2 area of Tph males completely in one sitting.

Packing by Iph fish could not be estimated as I surveyed only subsections of the grid. However it was

Figure 17. Territory boundaries of Tph *Sp. aurofrenatum* at sites M and B in 1978-9. Individuals are indicated by colours and numbers. The top of each grid points offshore (west).

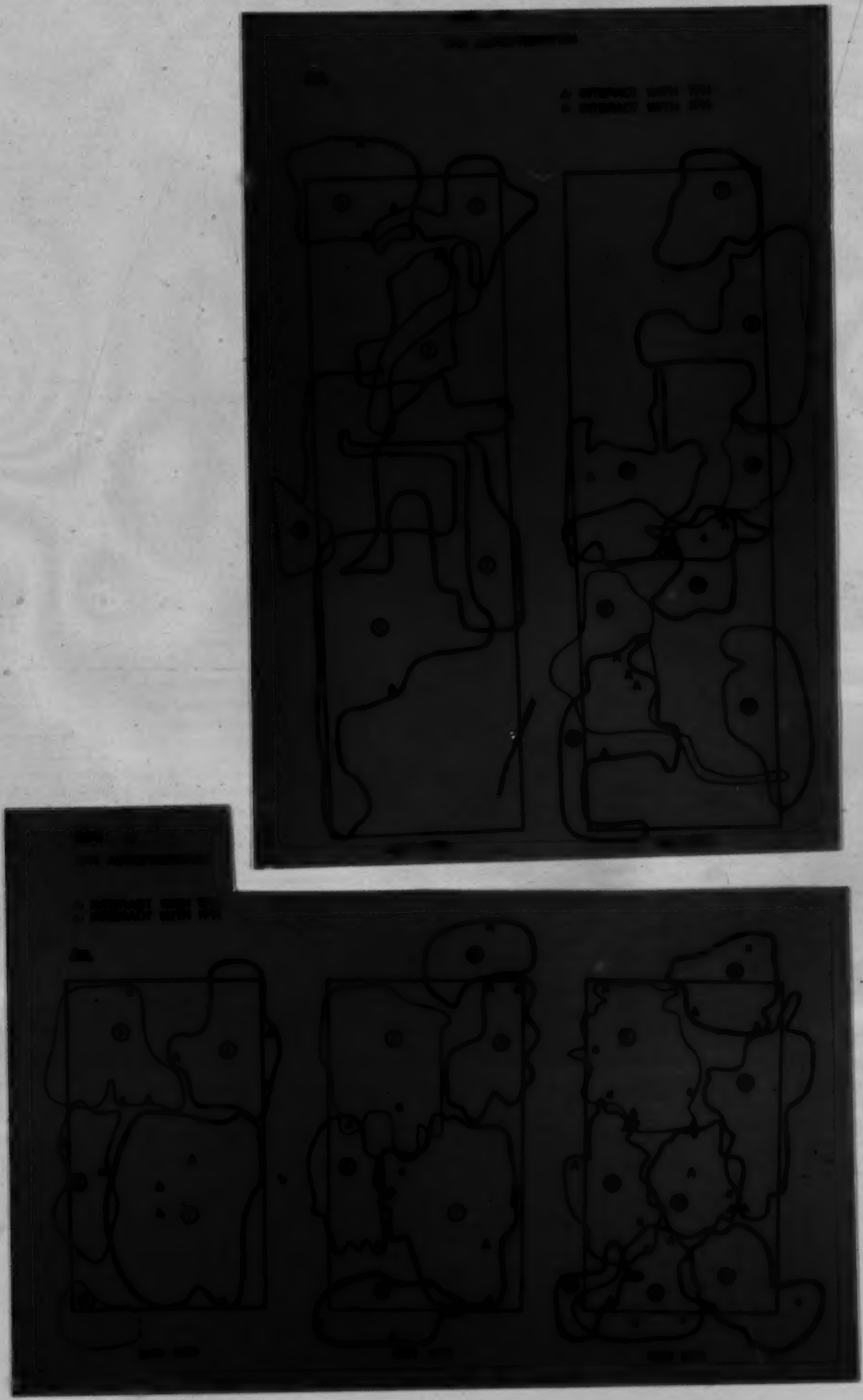


Figure 18. Territory boundaries of Tph *Sc. taeniopterus* at sites M and B in 1978-9. Individuals are indicated by colours and numbers. The top of each grid points offshore (west).

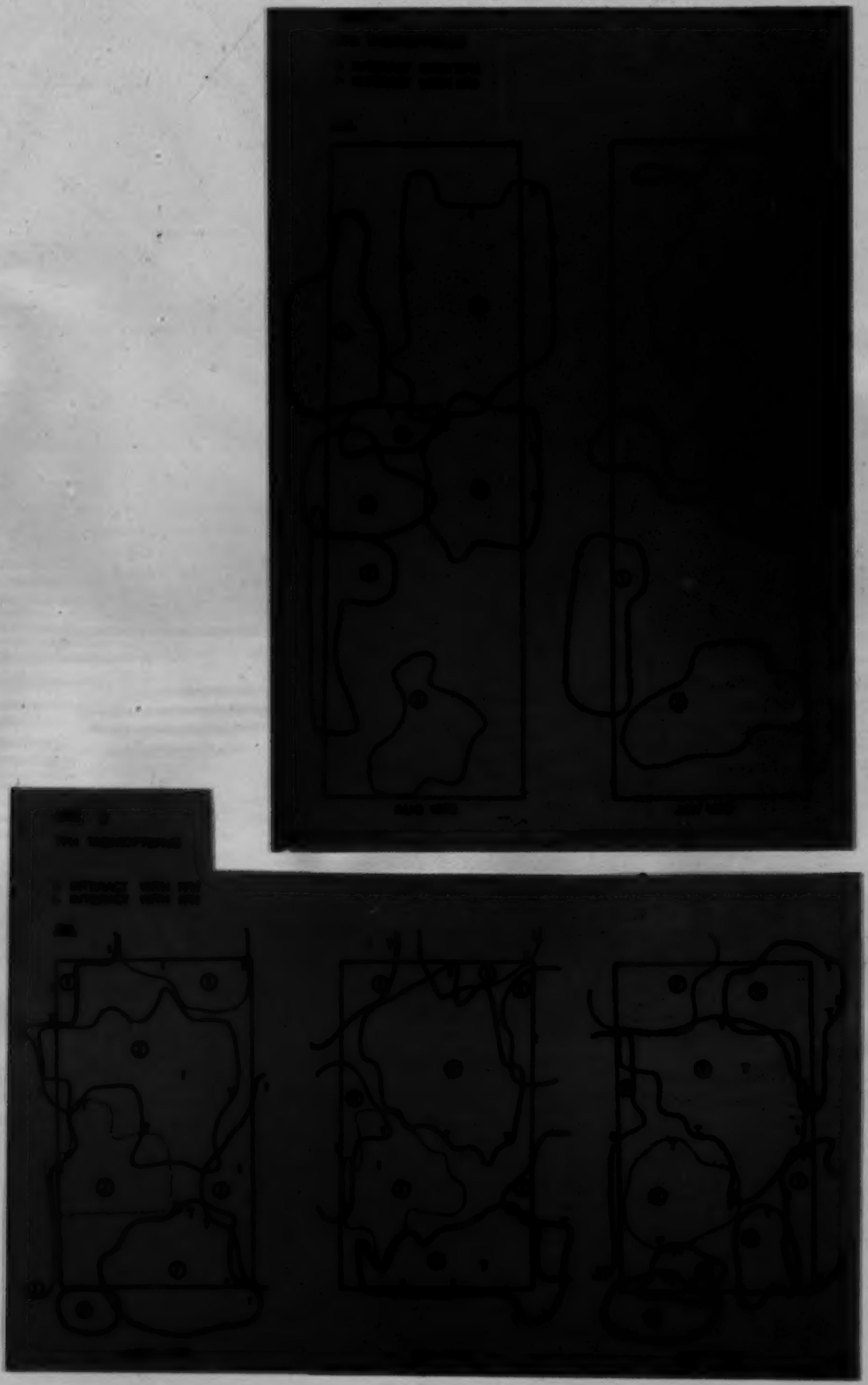


Figure 19. Territory boundaries of Tph *Sc. iserti* at sites M and B in 1978-9. Only a portion of the study grid was mapped. Individuals are indicated by colours and numbers. The top of each grid points offshore (west).

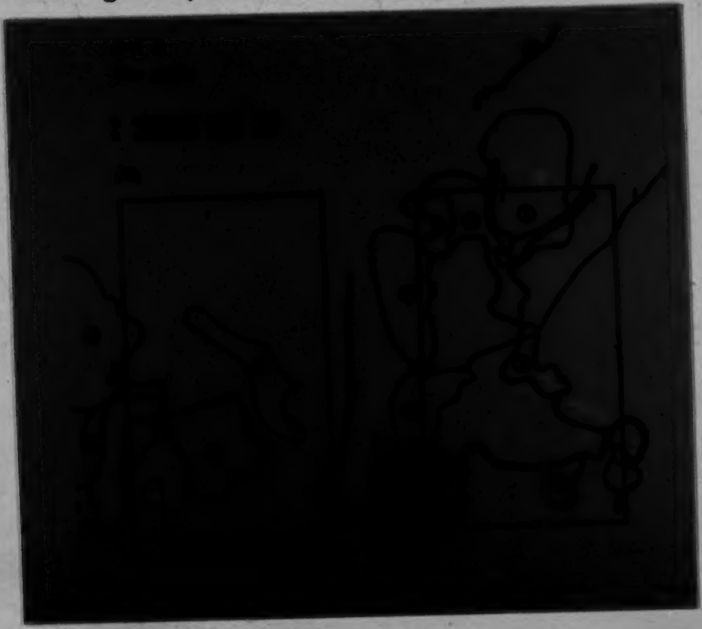


Table 24. The percent of each study area used by Tph of each parrotfish species (% usage), and the average overlap index (100 X no. of subquadrats shared/no. of samples/% usage). Data taken from computer maps (Appendix 2).

	Site M	Site A	Site B	Site P
Sp. aurofrenatum:				
Mean % usage	56	86	89	94
Overlap index	7.7	2.0	2.5	3.7
Sc. taeniopterus:				
Mean % usage	49	92	79	81
Overlap index	2.1	2.6	2.7	1.9
Sc. iserti[1]:				
Mean % usage	41	ND	85	95
Overlap index	6.8		3.7	4.3

[1] Total based on a subsection of study area.

probably similar to Tph packing. Home range maps of Iph fish at site M (Appendix 2, Figures 24 to 26) showed expanses of empty space, where I saw no Iph during the survey. Offshore, the home range boundaries of Iph corresponded to those of Tph (see below), so large empty spaces were unlikely.

Permanence

To qualitatively assess the permanence of space use patterns over long periods of time (6 months), I inspected both hand-drawn (Figures 17 to 19) and computer maps (Appendix 2). Short-term (24 to 72 hours) changes in individuals' boundaries were investigated in the same way. I could not measure long-term changes for fish at site A, or for Iph, as they were observed in only one sample period. However, the analyses of spatial distributions (Chapter 4) showed that distribution patterns of populations (primarily Iph), did not vary from month to month.

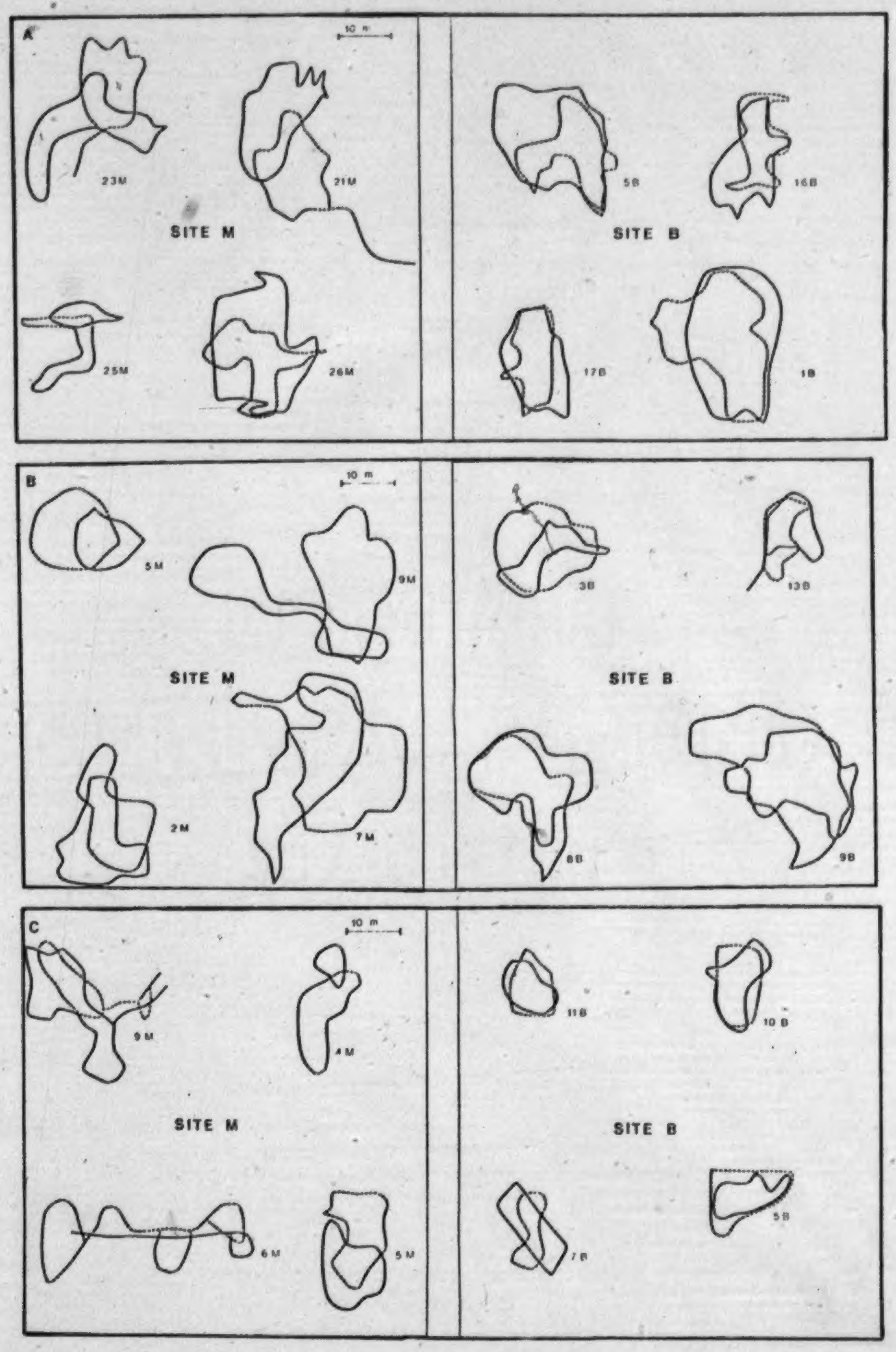
The boundaries at the offshore sites were stable for *Sp. aurofrenatum* and *Sc. taeniopterus*, with only slight adjustments in their positions over time (Figures 17, 18). Disappearance of an individual occasionally resulted in subdivision of his former territory by newcomers and neighbours as described in the previous chapter, but more often did not, and the newcomer's boundaries were almost identical to his predecessor's. The situation for *Sc. iserti* was less clear-cut as individuals remained for shorter periods of time. The one male (#7) who had remained at site B shifted slightly in six months (Figure 19). Of the two individuals remaining at site P, one held identical boundaries and the other shifted into a different territory (Appendix 2). The greater variation in boundaries of Tph *Sc. iserti* can be attributed to their more rapid turnover.

Boundaries inshore at site M were not permanent, and their positions within the study grid changed radically between study periods, particularly in *Sp. aurofrenatum* where a complete changeover of individuals had occurred (Figure 17), and in *Sc. iserti* as well (Figure 19). Those *Sc. taeniopterus* that remained at site M did not shift much, although one (#9) expanded and subsequently moved southwest off the area (Figure 18).

There was little evidence that particular areas at site M were consistently avoided by Tph, although some were used more often than others (see previous chapter). A 300 m² section of finger coral which adjoined a rubble field was not exploited by *Sp. aurofrenatum*. A section of rubble in the central part of the site was not used by Tph *Sc. taeniopterus*, although other similar sections were. *Sc. iserti* was observed only in the inshore half the grid, but did not avoid any zone. Territory maps made in 1976-7 confirmed this fact; territories shifted extensively but without pattern over time.

Short-term shifts in boundaries were also more extensive at site M (Figure 20). At the offshore sites, the boundaries transcribed after each sample were never identical, but they were concentric and similar in shape. At

Figure 20. Short-term changes in boundaries of Tph movements. Solid and dashed lines are boundaries for same individuals measured 24 to 96 hours apart at sites M and B. A)*Sp. aurofrenatum*; B)*Sc. taeniopterus*; C) *Sc. iserti*. The individual's identification number is shown.



site M, both the shape and geometric centre changed. Territories at site M were spatiotemporal (Wilson, 1975), i.e. they shifted from day to day although slight overlaps remained. *Sc. taeniopterus* varied less between sites in this respect than *Sp. aurofrenatum* or *Sc. iserti*.

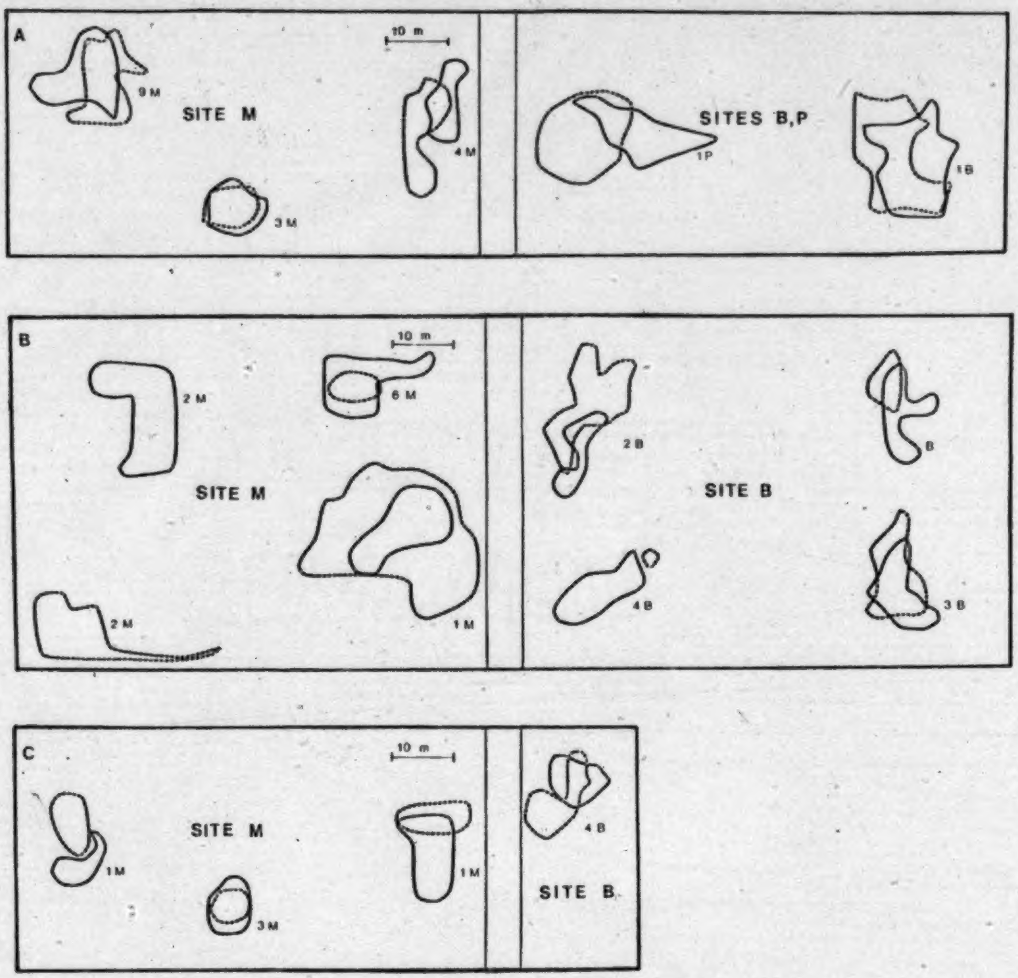
Iph fish showed few differences between sites in boundary permanence, although interpreting results was difficult because of the small numbers of individually recognizable fish. At site M, both shifting and fixed home ranges were seen in all three species (Figure 21). *Sp. aurofrenatum* shifted less than the other species at all sites. The same was true offshore; Iph individuals did not use identical areas each time although they remained in the same general area.

Exclusiveness

The analysis of overlap between individuals allows characterization of their social system. I will first discuss intra-phase and inter-phase overlaps of conspecifics and then will consider interspecific overlaps.

Tph *Sp. aurofrenatum* and *Sc. taeniopterus* used their space exclusively with two exceptions: *Sp. aurofrenatum* at site M, and transforming *Sc. taeniopterus* at all sites. These cases are discussed below. *Sc. iserti* allowed overlap at all sites, and males that were clearly resident tolerated transients or neighbours inside their boundaries (Figure 19). Territory compression during spawning was noted in this species by Barlow (1975), although territorial Tph in

Figure 21. Short-term changes in boundaries of Iph. Solid and dashed lines are boundaries for same individual measured 24 to 192 hours apart at sites M, B or P. A) *Sp. aurofrenatum*; B) *Sc. taeniopterus*; C) *Sc. iserti*. The individual's identification number is shown.


A
10 m
9 M
SITE M
4 M
3 M
SITES B,P
1P
1B
B
10 m
2 M
6 M
SITE M
1 M
2 M
2B
B
SITE B
4B
3B
C
10 m
SITE M
1M
3M
1M
4B
SITE B

Panama apparently are always aggressive to Tph intruders (Robertson et al., 1976). My data were insufficient to test whether Tph *Sc. iserti* were more exclusive when spawning, but this seems possible. Tph *Sc. iserti* were prone to leave their areas and swim off in a directed fashion (see Figure 19). These 'excursions' occurred at all sites, but were especially common at site M. There, where packing was looser, fish could have been moving between several disconnected sections of a home range. This was unlikely in the intensively used offshore areas, but fish with their own defended areas may have regularly visited others' territories. My own data are insufficient to test whether excursions were more likely at certain times of the day (e.g. outside spawning times) but this would be worth investigation.

There were differences between sites in overlap. I estimated Tph-Tph overlap at each site by counting the number of subquadrats shared per individual sample and dividing it by the percent usage (Table 24). Overlap between Tph *Sc. taeniopterus* was low at all sites. Both *Sp. aurofrenatum* and *Sc. iserti* had the highest overlap indices at site M, where there were large amounts of space left empty, and what was used was shared. These overlaps were not the result of fish using the same space at different times. Overlapping Tph often fed or swam together. This is not surprising in *Sc. iserti* whose gregarious nature is well known (Ogden and Buckman, 1973; Barlow, 1975; Itzkowitz, 1974, 1977a).

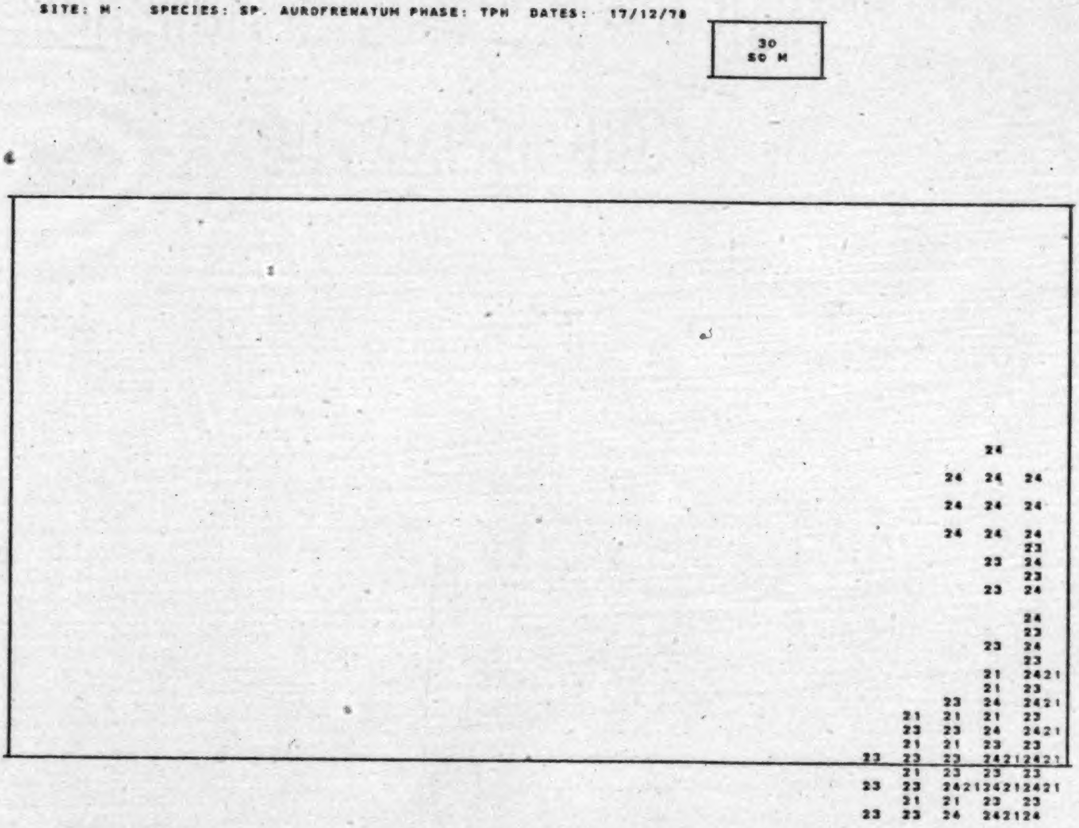
Gregarious Tph *Sp. aurofrenatum* have not yet been described. However, Randall and Ormond (1978) briefly mentioned overlapping territories of Tph *Sc. ferrugineus* in the Red Sea. These authors stated that one large male was usually dominant. In Barbados, such alliances involved two (on one occasion, three) Tph males who swam and fed together (Figure 22). I saw 15 alliances between Tph *Sp. aurofrenatum* at site M over the course of the study. One large male (#19 - SL 190 mm) was involved in five between November, 1978 and April, 1979. Alliances lasted from several days to four weeks. They were never seen at any of the other sites. Six occurred between males in the staghorn coral zone, eight took place in the inshore rubble and small coral heads zone, and one pair was seen in the deeper pillar coral zone (Figure 3). Most of the *Sc. iserti* overlaps occurred in the rubble zone too (Figure 19).

In all *Sp. aurofrenatum* alliances, one Tph, larger than the other, was dominant. Interactions between the pair were at a low level of aggression. The dominant Tph followed and supplanted the subordinate and the subordinate moved aside or arched submissively, sometimes turning an Iph-like striped pattern (see Barlow, 1975). In the one triplet seen (Figure 22), the interactions were two-way: the larger Tph dominated the medium one but ignored the small Tph, and the medium one dominated the small one. Pairs swam together, their territory boundaries changed over time in the same way

Figure 22. Computer map of a three-way alliance between a large (#24 - SL ca. 165 mm), medium (#23 - SL 144 mm) and small (#21 - SL 132 mm) Tph *Sp. aurofrenatum* at site M. All were sampled on the same dive. The offshore (west) end is at the left of the figure.

```
SITE: M    SPECIES: SP. AUROFRENATUM PHASE: TPH  DATES:  17/12/78
INDIVIDUAL      DATE      MINUTES WATCHED    AREA ENCLOSED (SQ M )
    21        17/12/78          11.5                64
    23        17/12/78          13.5               181
    24        17/12/78          17.0               175
```

SITE: M   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 17/12/78

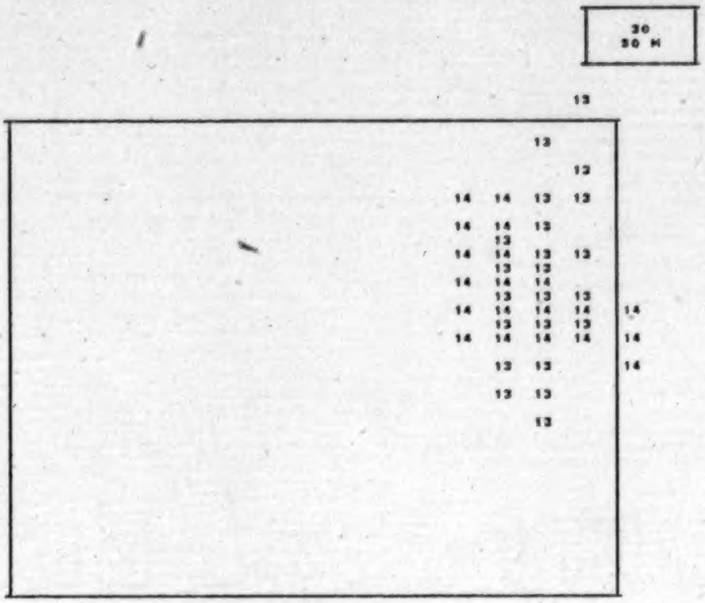


during the alliance and both fish defended the same border. Two alliance members (#21, #23) later shifted apart and began interacting aggressively (Figure 17). In July, 1977, interactions between adjacent pairs were observed; the like-sized fish displayed to one another but ignored the other alliance member. Males that had been pair members (one had been dominant, one subordinate) did spawn, although not when part of an alliance. Members of alliances did not disappear from site M at the same time; some remained longer than other partners and formed new bonds or stayed solitary. Dominant and subordinate Tph *Halichoeres maculipinna* share space, although subordinates remain for a long time, and fight to take over when a dominant disappears (Thresher, 1979a).

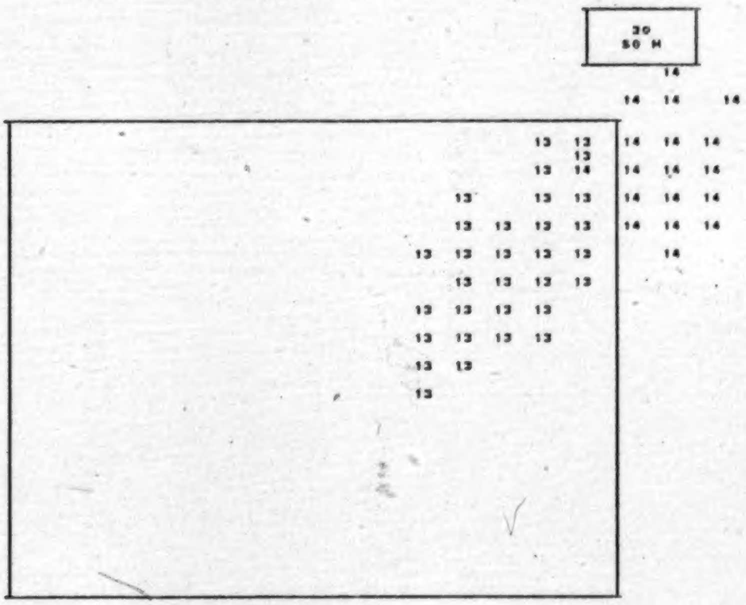
Newly transformed Tph *Sc. taeniopterus* shared space. I saw three such fish (#10, #11, #12 - Appendix 2) in the offshore end of site M, and two (#13, #14 - Figure 23) at site B. These groups also formed dominance hierarchies, although size differences were not so apparent. Both dominant fish (#10 at site M; #13 at site B) were further advanced in their colour change than the subordinate(s). These alliances gradually terminated as the fishes' Tph colours developed. After two weeks, one of the site M triplet had shifted northwards, the other subordinate had moved south. At site B, the subordinate (#14) shifted eastward. It later took up residence south of the other male (see Figure 18).

Figure 23. Sharing of space by two transitional *Sc. taeniopterus* at site B, and their shift apart two weeks later after Tph colour was more developed. Positions are indicated by the individual's identification number. The offshore (west) end is at the left of the figure.

SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 29/ 3/79



SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 14/ 4/79 TO 18/ 4/79



Space was not held exclusively by Iph fish (Figures 24 to 26) which formed a size-dependent dominance hierarchy. Aggression between differently-sized Iph was low-level; the larger fish supplanted or nipped at smaller ones who arched and moved away. Like-sized fish did exclude one another, and what appeared to be border interactions with fin erections, tailstands, and even mouth-to-mouth contacts were seen occasionally at all sites.

Iph fish offshore formed harems, i.e. the boundaries of their home ranges were enclosed within that of a Tph male (Figure 24 to 26). This was verified for all three species at sites B and P and for *Sp. aurofrenatum* at site A. It was probably true for *Sc. taeniopterus* there as well. Yellowfin Iph *Sc. iserti* were harem members, but some pale-finned Iph moved across Tph boundaries and were perhaps Iph males. One Iph *Sp. aurofrenatum* at site B ('O', Appendix 2) overlapped two males' boundaries but this was a spot where one Tph (#1) had retracted his border. Thus, males may 'lose' females if their territory shrinks. Another Iph at site P took a 20 m excursion outside her Tph's borders during one sample. Several Iph and Tph displayed to her, although not as if she were a transient (see pages 125-129), and she was back on her home range the next day.

No harems were found in the area surveyed at site M in *Sp. aurofrenatum* or *Sc. iserti*. Some Iph had home ranges overlapping the territories of several males, others dwelt in areas claimed by no Tph (Figures 24, 26). A few Iph *Sc.*

Figure 24. Home range boundaries of Iph *Sp. aurofrenatum* at sites B and M, in relation to the boundaries of overlapping Tph territories. The offshore end is at the top of the figure.

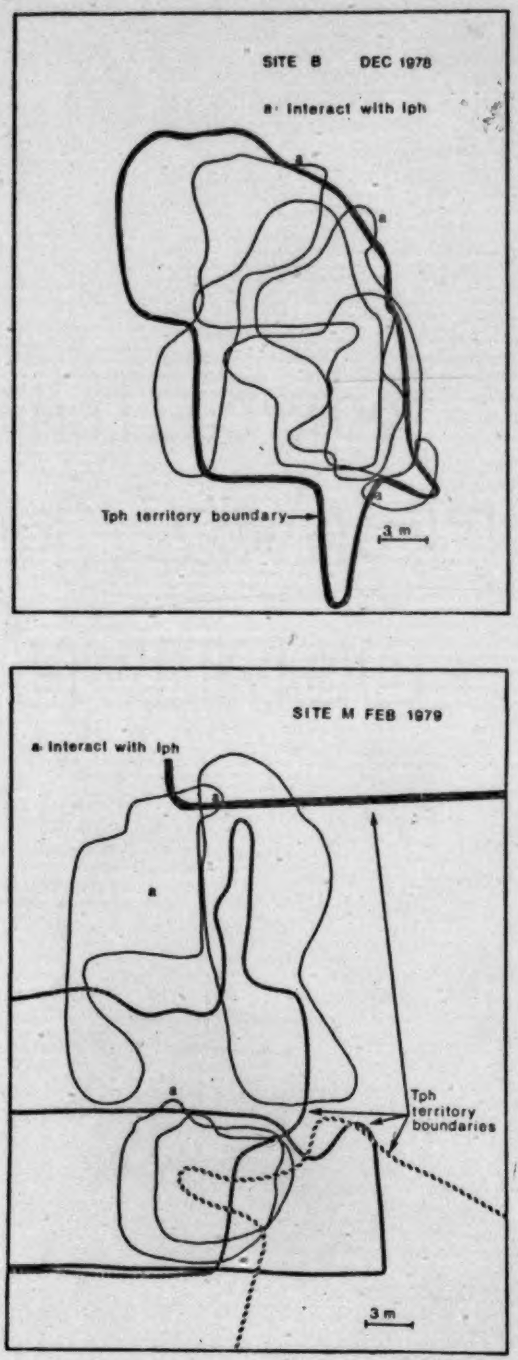

SITE B DEC 1978
a- interact with Iph
a
a
a
Tph territory boundary
3 m
SITE M FEB 1979
a- interact with Iph
a
a
a
Tph territory boundaries
3 m

Figure 25. Home range boundaries of Iph *Sc. taeniopterus* at sites B and M, in relation to the boundaries of overlapping Tph territories. The offshore end is at the top of the figure.

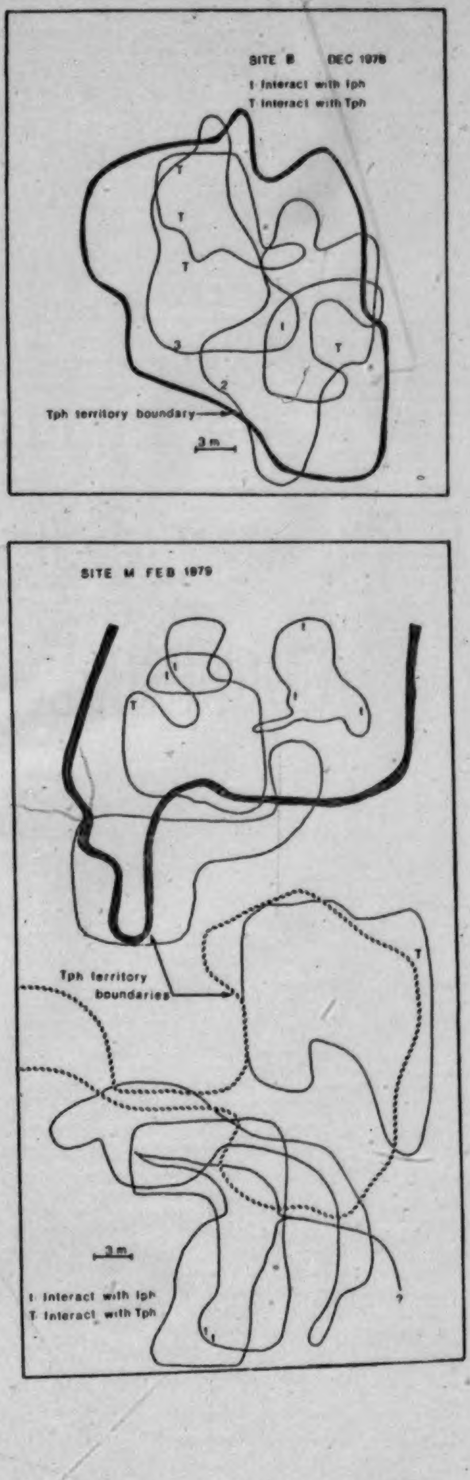
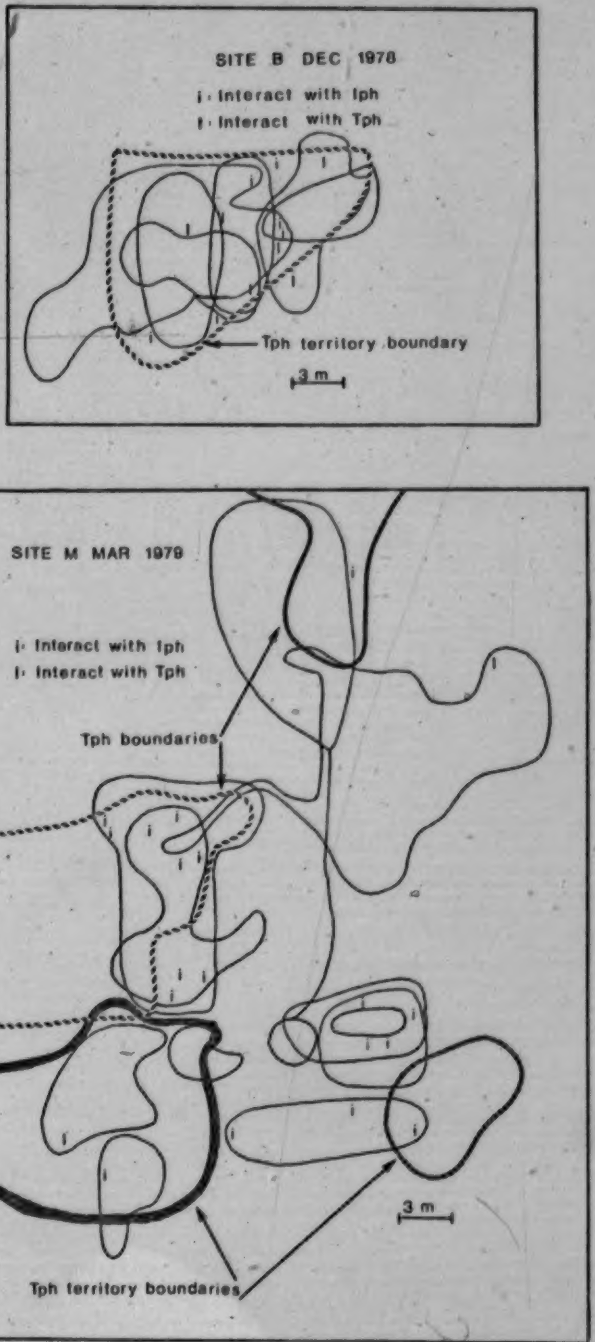

SITE B DEC 1978
I Interact with Iph
T Interact with Tph
T
T
T
3
2
I
T
Tph territory boundary
3 m
SITE M FEB 1979
I
I
T
I
I
I
Tph territory boundaries
T
3 m
I Interact with Iph
T Interact with Tph
I

Figure 26. Home range boundaries of Iph *Sc. iserti* at sites B and M, in relation to the boundaries of overlapping Tph territories. The offshore end is at the top of the figure.


SITE B DEC 1978
i - Interact with Iph
I - Interact with Tph
Tph territory boundary
3 m
SITE M MAR 1979
i - Interact with Iph
I - Interact with Tph
Tph boundaries
3 m
Tph territory boundaries

taeniopterus lived entirely within a Tph male's borders at site M, although most ranges bore no relation to Tph boundaries (Figure 25).

The social systems of all three species can be characterized thus. At offshore sites males defended permanent, exclusive, closely packed territories from conspecific Tph although *Sc. iserti* tolerated more overlap than the other species. Iph females dwelt in a size-dependent dominance hierarchy in harems within the Tph boundaries, and may have excluded like-sized fish. Judging from observations and grid surveys (Table 6), there were ca. 3 to 5 Iph females per harem. Some Iph *Scarus*, perhaps males, wandered freely between harems. Inshore, Tph *Sc. iserti* and *Sp. aurofrenatum* held spatiotemporal territories, and often shared space. Tph *Sc. taeniopterus* varied least between sites in this respect. Iph fish inshore had home range boundaries that were independent of Tph males', although some Iph *Sc. taeniopterus* were maybe haremic.

The three species studied, *Sp. aurofrenatum*, *Sc. iserti*, and *Sc. taeniopterus* did not subdivide space interspecifically at any site. This agrees with the analysis of grid survey sightings (Chapter 5) which showed many positive correlations between them. Perusal of territory maps (Figures 17 to 19, Appendix 2) showed that boundaries of Tph territories overlaid one another with no apparent pattern. The same was true for Iph fish which were surveyed in subsections of the study area. Perspective views of three-dimensional space-time graphs reinforced this conclusion (Figures 27, 28). The UBC-SURFACE program graphed the average percent of time spent by a species in each portion of the study area during one sample period. While species did not use space in identical fashions, some spending more time in parts of the grid than others, neither did they use it in contrasting ways. Species moved about each study area quite independently of one another, and interspecific aggression, which occurred rarely (Table 16), did not result in temporal partitioning of space.

Home range and territory size

Fish used differing amounts of space, depending on their species, phase and which site they inhabited (Table 25). Values in this table are the average amounts of space enclosed by the fish's movements during an observation period. Because territories at site M were spatiotemporal and changed greatly in shape and position from day to day (Figure 20), I used the amount of space enclosed during a sample as a measure of each fish's territory or home range size. Since borders at the offshore sites varied little from day to day, these values estimated the sizes of permanent territories or home ranges there reasonably well. The values in Table 25 agree with previously published ones for scarids in other parts of the world (Bruce, 1978; Randall and Ormond, 1978). The area enclosed during a sample did depend on the length of the observation period for all but Iph *Sc. iserti*, but appeared to level out for the other groups after

Figure 27. Overall pattern of space utilization by all fish sampled for activity budgets at site M in early 1979 formed by plotting the percent of time spent by a species in each subquadrat of the study area. Note that Tph *Sc. iserti* and Iph of all species were sampled in portions of the grid; flat areas do not imply that no fish of these groups spent time there.

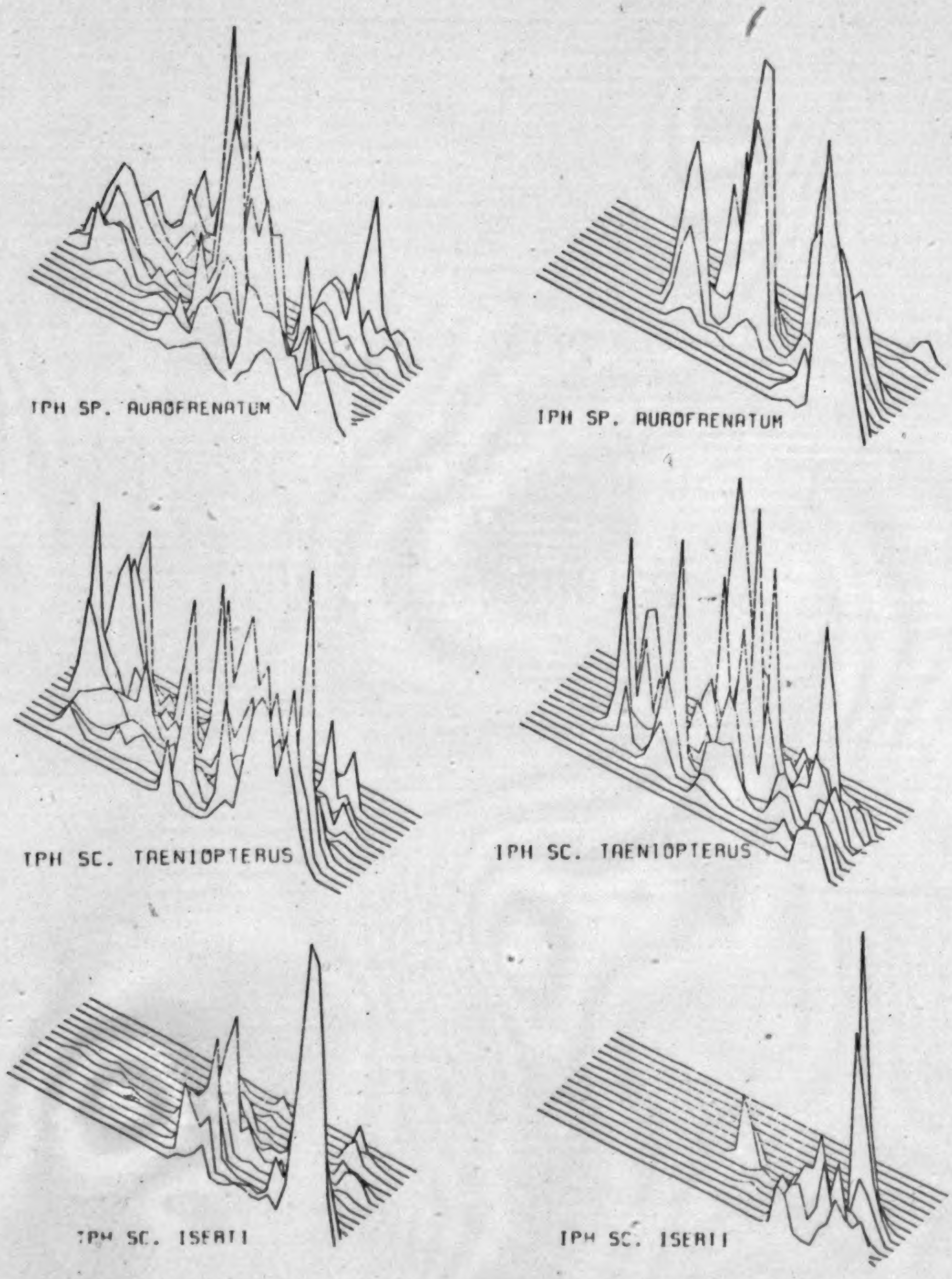
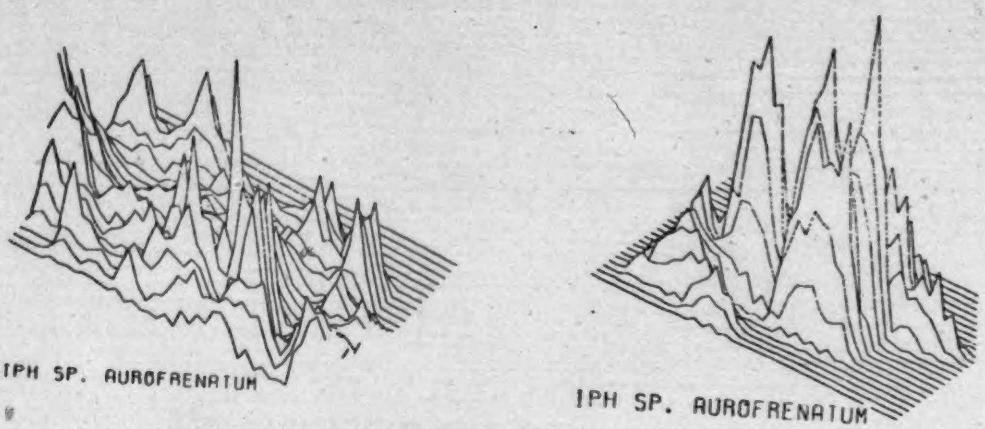
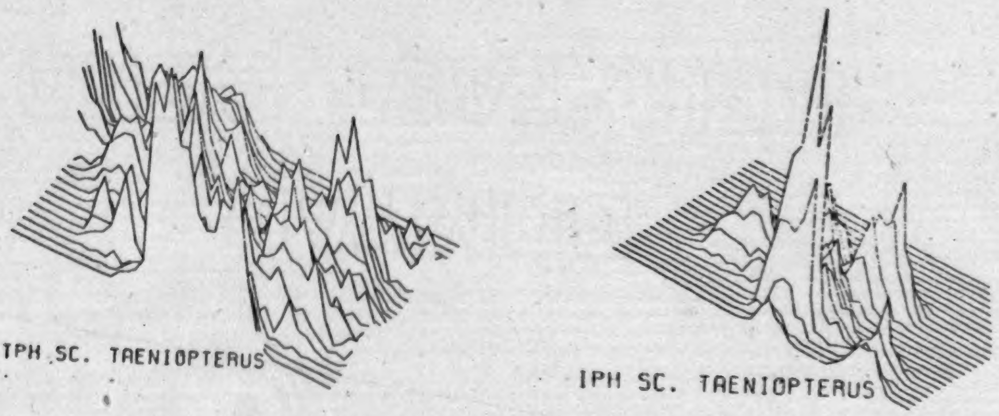


Figure 28. Overall pattern of space utilization by all fish sampled for activity budgets at site B in late 1978 formed by plotting the percent of time spent by a species in each subquadrat of the study area. Note that Tph *Sc. iserti* and Iph of all species were sampled in portions of the grid; flat areas do not imply that no fish of these groups spent time there.



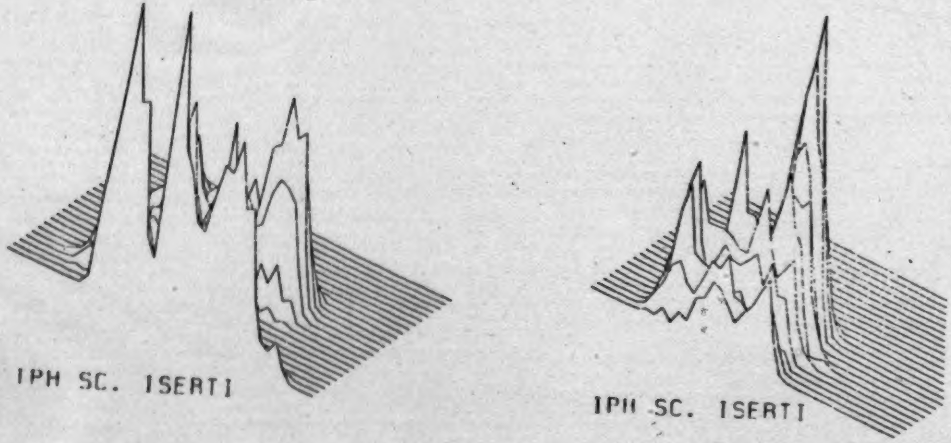
IPH SP. AUROFRENATUM

IPH SP. AUROFRENATUM



TPH SC. TAENIOPTERUS

IPH SC. TAENIOPTERUS



IPH SC. ISERTI

IPH SC. ISERTI

Table 25. Average area in m^2 enclosed by a fish's movements during an observation period. Only samples lasting at least 10 minutes are considered here. S.D.: standard deviation. n: sample size.

Species:	Site M	Site A	Site B	Site P	Overall
Iph *Sp. aurofrenatum:*					
Mean	**88.9**	**39.4**	**99.0**	**67.1**	**91.4**
S.D.	32.4	22.1	36.6	48.7	38.3
n	26	5	22	12	56
Tph *Sp. aurofrenatum*:					
Mean	**141.8**	**142.6**	**215.2**	**175.8**	**188.5**
S.D.	95.7	60.8	106.6	56.0	99.6
n	39	16	111	32	198
Iph *Sc. taeniopterus*:					
Mean	**116.0**	**ND**	**73.9**	**53.5**	**93.3**
S.D.	84.3		30.5	22.2	69.2
n	25		13	8	46
Tph *Sc. taeniopterus*:					
Mean	**158.7**	**107.4**	**224.5**	**256.3**	**193.3**
S.D.	78.5	43.5	104.4	125.6	105.9
n	45	21	61	23	150
Iph *Sc. iserti*::					
Mean	**36.5**	**ND**	**60.8**	**53.1**	**45.7**
S.D.	24.9		20.6	14.1	21.8
n	14		5	7	26
Tph *Sc. iserti*:					
Mean	**119.2**	**ND**	**108.1**	**78.2**	**99.4**
S.D.	76.2		44.0	29.5	51.7
n	17		27	27	71

10 to 20 minutes, which was within the range of my average observation time (Figure 29). However, to test for differences in home range size between sites, I used analyses of covariance (Snedecor and Cochrane, 1980) which adjusted for the effects of observation time.

All Tph males used more space than did Iph conspecifics (Table 25). The territories or home ranges of *Sc. iserti* were roughly half the size of the other species. With the exception of Iph *Sc. iserti*, home range or territory areas were significantly different between sites, but the trends depended on the species. In *Sp. aurofrenatum*, Tph territories and Iph home ranges were largest at site B. In Tph *Sc. taeniopterus*, territories were largest at site P, and smallest at site A, but Iph home ranges were largest at site M. Tph *Sc. iserti* had the smallest territories at site P.

I investigated whether fish size class or behaviour (i.e. percent of time spent in various activities) affected the area a fish used. In all but two cases, fish size class[11] had no effect on its home range or territory area. At site B, small Iph *Sp. aurofrenatum* used less space than larger ones ($F(2,31) = 4.7$, $P < 0.05$). Large Tph *Sp. aurofrenatum* at site M defended the least amount of space ($F(2,60) = 6.9$, $P < 0.01$), probably because they spent more time sitting (pg. 196; Table 30).

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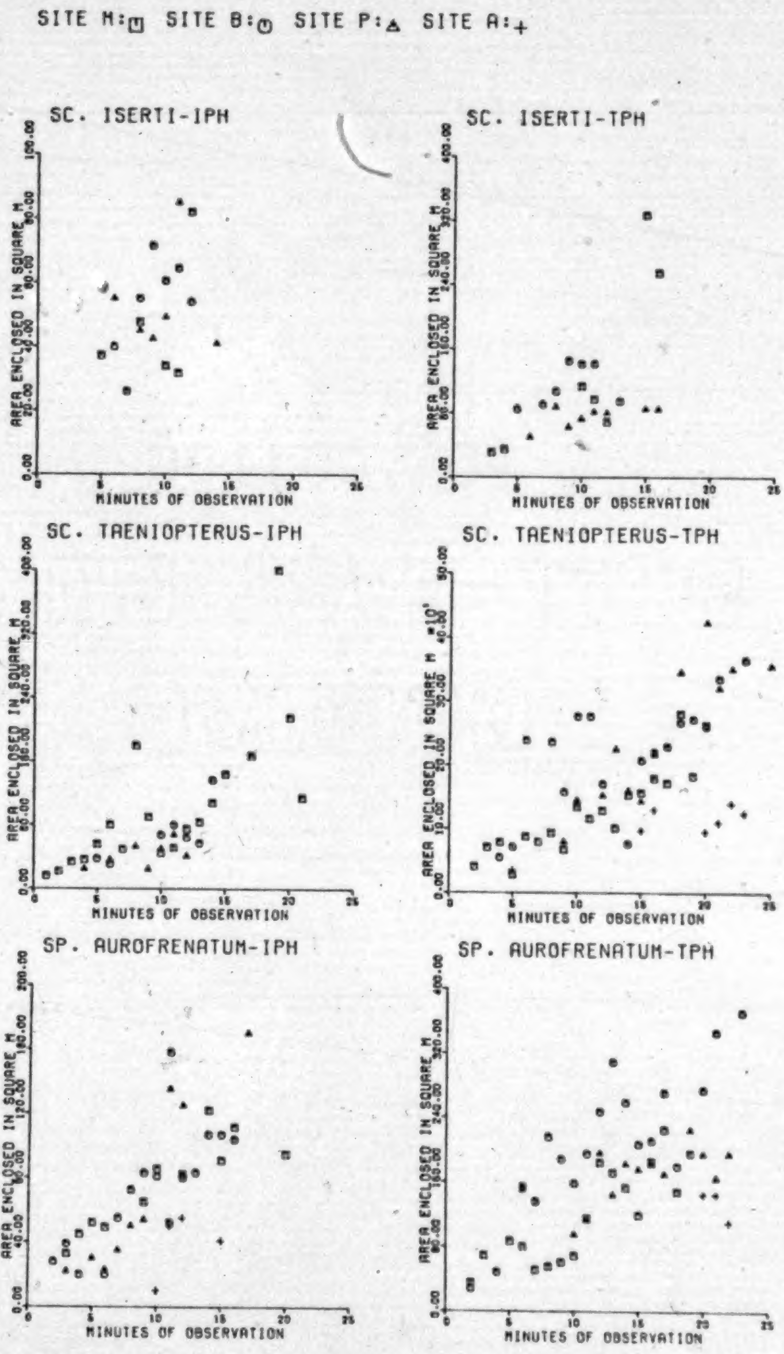
[11] Small, medium, large, with actual size ranges dependent on the species and phase.

Figure 29. Relation between area enclosed in m² by a fish's movements during an observation period, and minutes of observation.



The assumption that home range size should vary directly with animal size (McNab, 1963; Schoener, 1968; Dill, 1978), although apparently true for numerous animals with feeding territories, was not supported by my data. It could be argued that Tph required more space than Iph conspecifics because they weighed more (Table 27) and thus had greater energy requirements. This seemed unlikely since Tph males uniformly spent less time feeding than Iph fish (Figure 32). Moreover, with the exception of *Sc. iserti*, the Tph territory:Iph home range size ratio exceeded the ratio of their weights. This difference was especially marked at the barrier reef sites. While fish size may have some effect on a species' space needs- *Sc. iserti*, the smallest scarid in this study (Randall, 1968; Table 27), used the least amount of space- it did not directly determine an individual's home range or territory size at any study site.

Food supply and home range size are also often inversely related in fish (Slaney and Northcote, 1974; Dill, 1978; Ebersole, 1980; Hixon, 1980b; Larson, 1980a,b). However, the ranking of study areas with regards to food supply (Site M > Site B > Sites A and P, Chapter 3) was not the same as a species' ranking according to territory size (Table 25). Only Iph *Sc. iserti* had smaller home ranges at site M where food was most abundant but this difference was not significant. This hints that the amount of space used by parrotfish is not directly related to their nutritional needs. Iph fish, despite their large energy requirements for growth and reproduction, used less space than Tph males. Tph males appeared to be defending more space than was necessary to supply them with food.

The intrusion rate by other males at the offshore sites (Figure 14) did show some relation to territory size. Tph *Sc. taeniopterus* territories were smallest and intruders most common at site A, and the reverse was true at site P. Tph *Sc. iserti* intruders were perhaps more common at site P as well (see above), where territories were smallest. The relation was not as clear for Tph *Sp. aurofrenatum*, as territories were small at site A yet intruders there were not abundant. Residents' small territories at site A probably resulted from the fact that these large males spent more time sitting motionless than on the barrier reef (see Table 30), and sitting time correlated negatively with territory size (Table 26). Territory size was lower at site P than at site B, which had fewer intruders (Figure 14).

Other behaviours also affected territory or home range size. Fish that spent more time swimming generally had larger territories (Table 26). Since feeding correlated negatively with swimming (Figure 33), most fish that fed more had smaller territories or home ranges (Table 26). Thus, maintaining a large territory or range exacted a cost from the fish in the terms of the time it could allot to feeding. The area defended increased with duration of occupancy for Tph *Sc. taeniopterus* at site M ($r(15) = 0.59$, $P < 0.05$), and Tph *Sp. aurofrenatum* offshore (site P, $r(8) =$

Table 26. Partial correlation coefficients (controlling for minutes of observation) between time spent in different activities and area enclosed by fish's movements. Degrees of freedom in parentheses. Dams.: damselfish. *: P < 0.05; **: P < 0.01; ***: P < 0.001. Subm.: submission. Misc.: miscellaneous. Other: other scarid species.

	Behaviour (% time spent in each activity):								
	Swim	Feed	Sit	Interact with				Subm.	Misc.
				Dams.	Iph	Tph	Other		
Iph *Sc. iserti*									
Site M(18)	0.73***	-0.68***	-0.47*	0.42*	-0.23	0.28	-0.22	-0.25	0.12
Site B(10)	0.44	-0.40	0.10	-0.49	-0.34	-0.23	0.18	0.10	0.47
Site P(10)	0.51*	-0.25	-0.03	-0.62*	-0.19	-0.16	0.77**	-0.04	0.04
Tph *Sc. iserti*									
Site M(18)	0.43*	-0.54**	-0.23	0.32	0.25	-0.02	0.02	ND	0.17
Site B(31)	0.13	-0.61***	-0.02	-0.31*	0.37*	0.47**	0.66***	-0.22	0.42**
Site P(30)	0.21	-0.55***	-0.44**	-0.04	0.30*	-0.29	0.52***	-0.25	0.12
Iph *Sc. taeniopterus*									
Site M(43)	0.33*	-0.29*	-0.16	0.20	-0.11	0.28*	0.06	-0.25*	-0.05
Site B(14)	0.55*	-0.50*	-0.06	0.23	0.03	0.27	0.56*	-0.11	-0.07
Site P(16)	0.69***	-0.65**	0.25	0.70***	-0.03	-0.09	0.08	0.08	-0.02
Tph *Sc. taeniopterus*									
Site M(69)	0.32**	-0.42***	-0.03	0.38***	0.04	-0.17	0.04	-0.20	0.03
Site A(19)	0.37*	-0.49*	-0.17	0.21	0.29	0.18	0.02	ND	-0.09
Site B(67)	0.31**	-0.32**	-0.09	0.02	0.04	-0.04	-0.04	ND	0.13
Site P(21)	0.23	-0.47*	-0.44*	0.36*	0.09	0.20	0.08	ND	0.36*
Iph *Sp. aurofrenatum*									
Site M(34)	0.31*	-0.38*	-0.32*	0.40**	-0.12	0.08	-0.07	-0.33*	0.44*
Site A(2)	0.92*	0.87	0.30	-0.03	0.47	ND	ND	ND	-0.85
Site B(41)	0.30*	-0.26*	0.04	-0.28*	0.19	-0.11	-0.08	-0.26*	-0.04
Site P(9)	0.45	-0.06	-0.32	0.27	-0.03	0.42	-0.37	-0.17	-0.32
Tph *Sp. aurofrenatum*									
Site M(52)	0.35**	-0.35**	-0.37**	0.12	0.17	0.11	-0.20	-0.02	0.14
Site A(13)	0.58*	-0.41	0.50*	-0.19	0.39	-0.24	-0.03	ND	-0.26
Site B(127)	0.09	-0.14	-0.11	-0.04	0.12	-0.06	0.04	ND	0.73***
Site P(32)	-0.03	-0.04	-0.27	-0.03	0.15	0.09	0.17	ND	0.03

0.78, $P < 0.01$; site B, $r(44) = 0.40$, $P < 0.01$), which suggests that older, perhaps more experienced Tph can put pressure on their boundaries to expand them.

Fish that were more aggressive did not have larger territories, with the exception of both phases of *Sc. iserti* and Iph *Sc. taeniopterus* on the barrier reef: those with more interspecific interactions tended to have larger ranges (Table 26). This may indicate a synergistic effect of interspecific aggression on space used by *Sc. iserti* and *Sc. taeniopterus*, since these two species interacted most with each other (Table 16). Tph *Sc. iserti* on the barrier reef that interacted more with Iph conspecifics also had larger areas. Some Iph that were more submissive had smaller ranges. In some cases interactions with damselfish were related to larger territories, perhaps because damselfish attacks kept parrotfish moving. However, the effects of damselfish aggression were not consistent.

Parrotfish appear to be capable of considerable territorial expansion and compression. Yellowfin Iph *Sc. iserti* in Panama defended very small territories (10 to 12 m^2; Buckman and Ogden, 1973). Clavijo (1980b, and pers. comm.) reported a territory size of 80 m^2 for Tph *Sp. aurofrenatum* in Puerto Rico, while S. G. Hoffman (pers. comm.) measured sizes of 500 to over 1000 m^2 in Panama. These results underline the fact that territory size and food supply do not have a simple negative relation. The food supply in Panama was probably of higher quality and more abundant (pg. 238). The fact that Iph *Sc. iserti* had smaller territories there and at site M, hints that they may be food maximizers (Ebersole, 1980), which defend only enough space to meet their energy requirements. Tph *Sp. aurofrenatum* may be time minimizers (Hoffman and Stouder, 1980), which spend only enough time on feeding to meet their needs and invest the rest in social interactions. Hoffman and Stouder (1980) reported having experimentally increased the size of this species' territory by addition of food, as did Ebersole (1980) for female *Eupomacentrus leucostictus*. Feeding territories usually contract when food is added (Slaney and Northcote, 1974; Simon, 1975). The relation between a species' space requirements and its food supply is obviously not a simple inverse one; obtaining food may be of secondary importance to some Tph males, particularly those dwelling offshore.

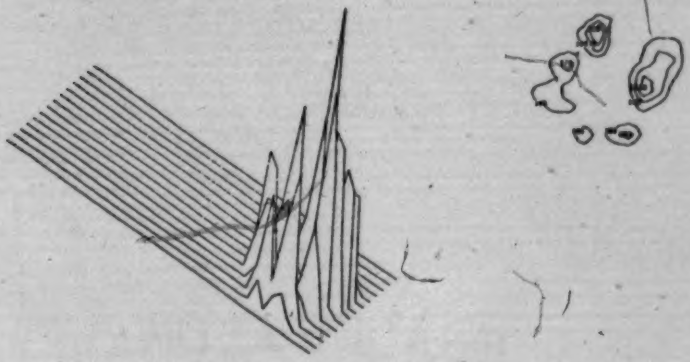
C. Use of space-individual patterns

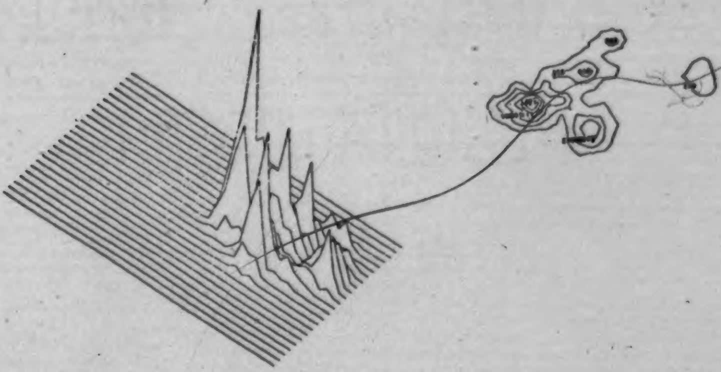
Individual parrotfish distributed their time differently over their home range or territory. Some moved between scattered points, stopping briefly here and there to feed. Others were more sedentary, remaining in one portion of the grid or returning repeatedly to it. In order to visualize their space use patterns better, I graphed the percent of time spent in each quadrat during one sample period using the UBC-SURFACE programs mentioned above. I made graphs for several samples of two to three individuals of each species and phase at every site. Only selected examples are shown here to illustrate the two different patterns observed (Figures 30, 31).

The scattered space utilization pattern (Figure 30) appeared as a series of separate peaks near the perimeter of the fish's range, surrounding a central trough where little time was spent. It was seen in Tph and some Iph *Sc. taeniopterus* at all sites, in all Tph and some Iph *Sp. aurofrenatum* offshore, and variably in both phases of *Sc. iserti*. An individual *Sc. iserti* offshore might show a scattered pattern one day followed by an intense space utilization pattern the next. Intense utilization patterns appeared as one or two tightly packed central peaks (Figure 31). All Tph *Sc. iserti* at site M and some Iph and Tph elsewhere, displayed the intense pattern, as did all Tph *Sp. aurofrenatum* at site M, and some Iph *Sp. aurofrenatum* at all sites.

An intense pattern could appear in fish that were exploiting a rich but patchy food supply so that the motivation would be to stay and use it before moving on (Warner, 1979). Fish at site M, which showed the intense pattern, were perhaps using space in this way. Site M had the richest food supply and most heterogeneous coral cover (Chapter 3). Parrotfish displaying the intense pattern did not give any evidence for a central activity centre or favoured areas used repeatedly day after day (e.g. Nursall, 1977; Gronell, 1980). Surface plots made on the same

Figure 30. Selected examples of scattered pattern of space utilization by individual fish. Graph on right is a contour map with lines connecting points where the same percent of time was spent. The graph on the left is a perspective view of the same surface with peaks were much time was spent.


IPH SC. TAENIOPTERUS #1, SITE M, 14 FEB 1979


IPH SP. AUROFRENATUM # 7, SITE A, 31 MAY .1979

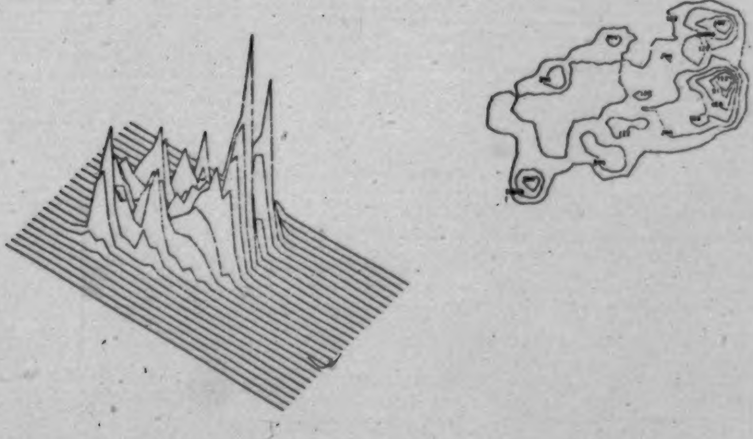
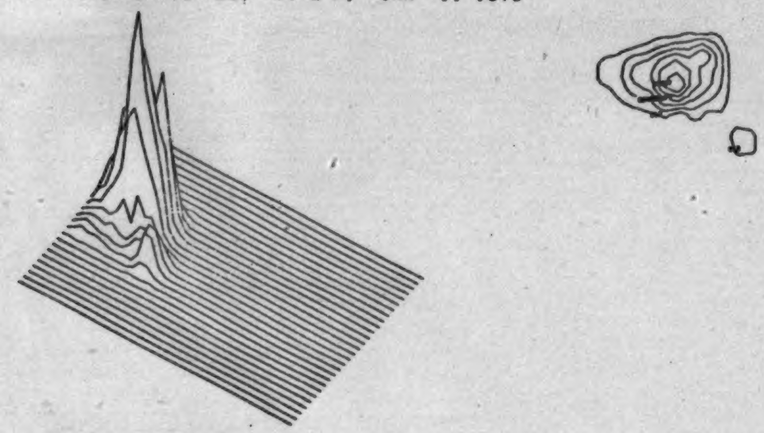
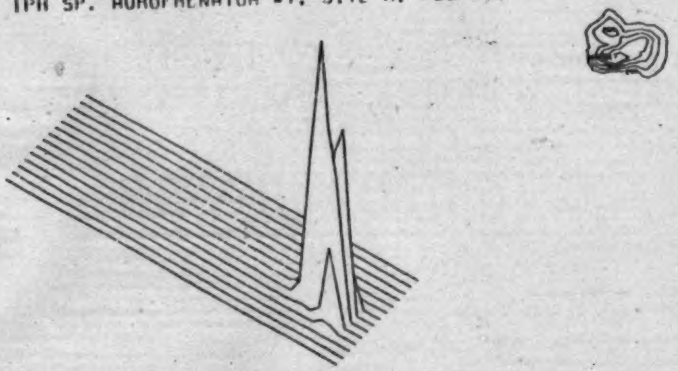

IPH SC. TAENIOPTERUS #8, SITE P, 11 SEPT, 1978

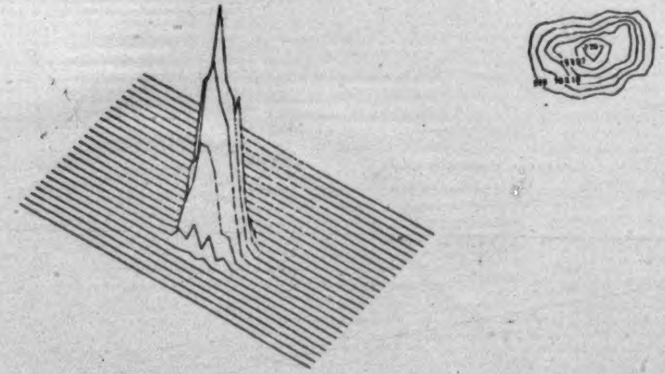
Figure 31. Selected examples of intense pattern of space utilization by individual parrotfish. See Figure 30 for explanation.



TPH AUROFRENATUM 25, SITE M. JAN 11 1979



IPH SP. AUROFRENATUM •7. SITE M. FEB 15. 1979



IPH SC. ISERTI •3. SITE B. 29 DEC 1978

individual at different times showed that the central peaks shifted from sample to sample, perhaps an indication than fish fed in different spots from day to day.

The peripheral peaks of the scattered pattern also varied between samples. This pattern could appear if fish were exploiting a less rich, more dispersed food source. The feeding mode used by the *Scarus* species of swimming, descending to feed, then moving on again (Barlow, 1975), could produce a scattered pattern when movements were constrained inside home range boundaries. However, fish exploiting evenly distributed resources should show a plateau, or no particular pattern of peaks. The fish with a scattered pattern clearly spent more time on their borders than centrally. This central trough is probably related to territorial defence and patrolling. Tph males may have to be continually present on their borders to prevent encroachment and loss of space. This explains in part why Tph *Sc. iserti* and Tph *Sp. aurofrenatum* at site M, which shared space with other Tph, showed the intense pattern rather than the scattered one: they were not patrolling their borders. It also explained why Iph patterns were variable. Some were territorial (e.g. yellowfin *Sc. iserti*), others were not. Territory or home range size also affected the pattern of space utilization only slightly. Fish with large territories (> 100 m²) tended to show the scattered pattern, although many with smaller ones did too. The fact that many parrotfish spent more time on their territory or home range boundaries than centrally is notable, for it meant that they placed a high priority on defence of space and left the central portions of their ranges relatively unexploited.

D. Summary

Parrotfish clearly used space in different ways, depending on their phase, species and the site they inhabited. Space was packed tightly offshore, but loosely inshore at site M by all species. Tph there were not excluded from parts of the reef by the damselfish *E. planifrons*; some of the most intensely used areas were central staghorn coral zones where this damselfish was abundant (compare Figures 3, 17 to 19, and 27, see Chapter 5). Iph fish at site M, however, may have been excluded from damselfish areas (Chapter 5).

Tph males all showed more variable boundaries at site M. The presence of contiguous, aggressive neighbours offshore may restrain Tph's movements and keep them from varying as much from day to day. Tph *Sc. taeniopterus* boundaries varied least of the species studied on a short-term basis at site M. Many of them were permanent residents there. Temporary residents were more weakly attached to specific areas. Some Iph fish at all sites had relatively constant borders, others changed between samples. Iph fish were probably less subject to aggression than Tph if they moved outside their home ranges, and thus were less constrained to one spot. Those that had fixed borders were perhaps haremic females, fish with variable boundaries were maybe Iph males. However, collections would be necessary to verify this. Iph *Sp. aurofrenatum* showed fewer boundary variations than the *Scarus* at all sites, a reflection of stronger site attachment.

All Iph tolerated overlap with others and dominated smaller conspecifics, although they excluded and behaved most aggressively towards like-sized individuals. This size-dependent territoriality needs more investigation as its function is unclear.

Of all three species, Tph *Sc. iserti* were most tolerant of other Tph in their territories, and frequently left their own to forage elsewhere. A study of such excursions in relation to spawning activity is required. Tph *Sc. taeniopterus* and *Sp. aurofrenatum* were more committed to continually defending their own territories, and only allowed overlap under special circumstances: newly transforming *Sc. taeniopterus* and differently sized *Sp. aurofrenatum* at site M. Both cases are related to reproductive activities. Transitional Tph *Sc. taeniopterus* did not spawn, and so were not rivals. They shifted apart as their transition was completed (Figure 23). Spawning was uncommon at site M (Table 33) which may explain why Tph *Sp. aurofrenatum* tolerated other males. Still it is not obvious why these fish shared space, and even defended common borders rather than moved into the expanses of empty space available. While a large, dominant, non-spawning, Tph male stood to lose little by allowing a small male within his borders, one wonders why the subordinate pair member would remain. The answer may be related to food. Most alliances occurred between fish in the staghorn coral and small coral heads zone where damselfish densities were high (Chapter 3). Small Tph, which would be more easily dominated by *E. planifrons* (Robertson et al., 1976; Waldner and Robertson, 1980), were perhaps less likely to be attacked by damselfish if accompanying a larger fish. Interaction rates with damselfish were highest for Tph *Sp. aurofrenatum* dwelling in these zones, although the difference was not quite significant ($F(3,75) = 1.9$, $P = 0.13$). Time spent interacting with damselfish was negatively correlated with feeding ($r(77) = -0.23$, $P < 0.05$).[12] However, the percent of time spent in damselfish interactions by sharing Tph males was 2.8 (n=11), below the overall average for site M (3.8 %, n=79), and the value for one small Tph (#21) increased from 2.3 % when sharing with two other males, to 9.6 % when he later became solitary. Sharing space may be one way that Tph *Sp. aurofrenatum* overcome damselfish aggression, and small males perhaps lose less from the occasional minor aggression directed at them by their dominants, than they gained from being able to feed on the rich algal turfs of *E. planifrons*.

In general, Tph territory size was related neither to fish size, nor to an area's food supply. This suggests that they are defending space for purposes other than feeding. The observation that some males formed feeding alliances perhaps to overcome damselfish aggression supports this. Tph territories offshore were perhaps smaller where intruders were more abundant. Maintaining a large area meant that fish had to swim more, feed and sit less, but not necessarily be more aggressive.

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[12] In Tph *Sc. iserti* at site M, which also commonly fed together, there was a similar relation ($r(31) = -0.33$, $P < 0.05$). There was no such effect for the other species.

The social system at site M was greatly different from the other sites where harems of Iph formed. Home range positions of Iph and Tph inshore were independent. Such variability in social systems is not surprising (see Buckman and Ogden, 1973; Ogden and Buckman, 1973; Barlow, 1975 for *Sc. iserti*) but it should alert researchers to the pitfalls of categorizing a species' social system as something fixed. Parrotfish clearly are capable of a wide range of social and space-related behaviour; this generality may be one reason for their great success on most reefs (Chapter 4).

An outcome of this analysis is the conclusion that the three species observed here do not compete among one another for space, nor do they use space in contrasting ways. Whether they exploit one spot intensively or move between scattered points appears to depend less on their species than on their spatial commitment (i.e. patrolling their border vs. not patrolling) or type of food exploitation. Elsewhere on the reef, herbivorous damselfish and blennies share space with little interspecific aggression (Nursall, 1981), yet conventional theory states that they should be competitors. The adaptations of reef fish which allow them to share space and food, often amicably, obviously require more investigation.

E. Parrotfish social behaviour - Use of time

The three parrotfish species studied intensively, *Sp. aurofrenatum*, *Sc. taeniopteus* and *Sc. iserti* did not subdivide space interspecifically, nor did they show interactive patterns in the time spent in parts of each study area. In short, they did not appear to be competing for space, which by classical reasoning is the limiting factor on reefs (Smith and Tyler, 1972; Fishelson et al. 1974; Sale,1975). However, a conclusion that these species were ecologically identical would be premature, for while they existed in the same space, they may have behaved differently within it. I compared the species' activity budget to determine whether they exploited the same environment in different ways. Because aggressive interactions maintain social and spacing patterns, I paid particular attention to the amount of time that each species allocated to aggression.

Analysis of activity budgets is important for another reason; it allows comparison of each species' behavioural response to the different ecological factors present at each study site. Labrids and scarids exhibit extensive behavioural flexibility, which allows them to make short-term adaptive responses to differing conditions (e.g. Warner and Downs, 1977; Warner and Hoffman, 1980b; Hoffman and Stouder, 1980; Dubin and Baker, 1981). My aim was to compare activity budgets of parrotfish among my study sites to determine:

1. which underlying ecological variables affected how these fish allocated their time to each activity,
2. how differences in activity budgets explained the variation in social systems between inshore (Site M) and offshore sites (A,B,P),
3. what ecological factors were the ultimate determinants of the social systems displayed by these parrotfish.

In this section I will compare each species' and phase's activity budgets and will discuss what other factors (fish size, duration of occupancy, time of day) might affect them. Below, I will discuss how they vary between sites.

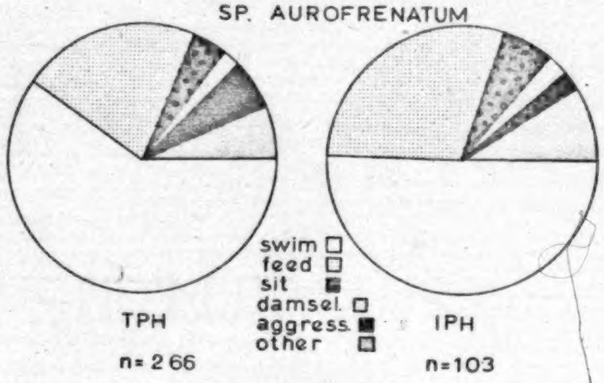
Overall activity budget

Activity budgets differed depending on a fish's species and phase (Figure 32). All parrotfish spent over 85 % of their time feeding and swimming, and time spent on these two activities correlated inversely (Figure 33). *Sp. aurofrenatum* spent the most time swimming, *Sc. iserti* the least. Both *Sc. iserti* and *Sc. taeniopterus* invested considerably more time in feeding, and fed at more rapid rates than *Sp. aurofrenatum*. Iph of all species spent 40 % more time than Tph in feeding, which was expected due to the greater energetic costs of producing eggs. However, Iph

Figure 32. Percent of time spent in different activities by parrotfish in Barbados. "Damsel." is % time being chased by damselfish. "Aggress." is percent of time interacting with other parrotfish. "Other" includes miscellaneous activities such as being cleaned, sitting under cover, and various body movements.

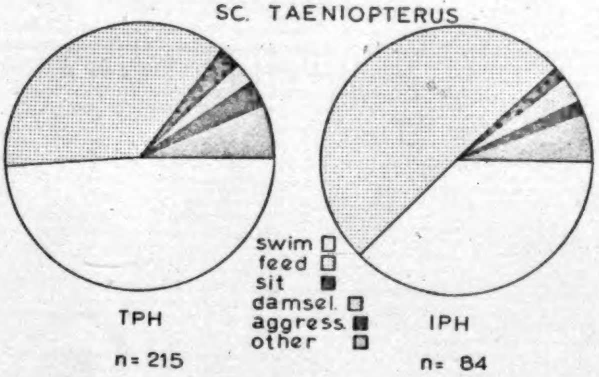
ACTIVITY BUDGET

SP. AUROFRENATUM



ACTIVITY BUDGET

SC. TAENIOPTERUS



ACTIVITY BUDGET

SC. ISERTI

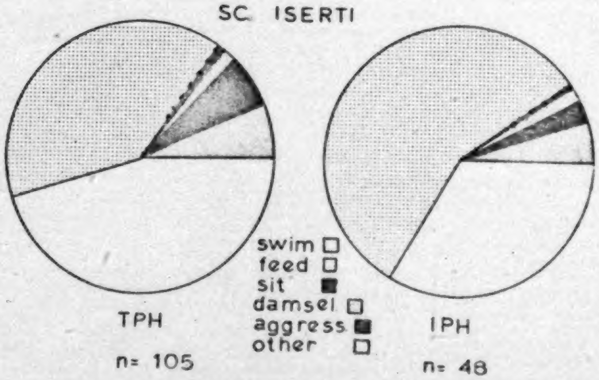
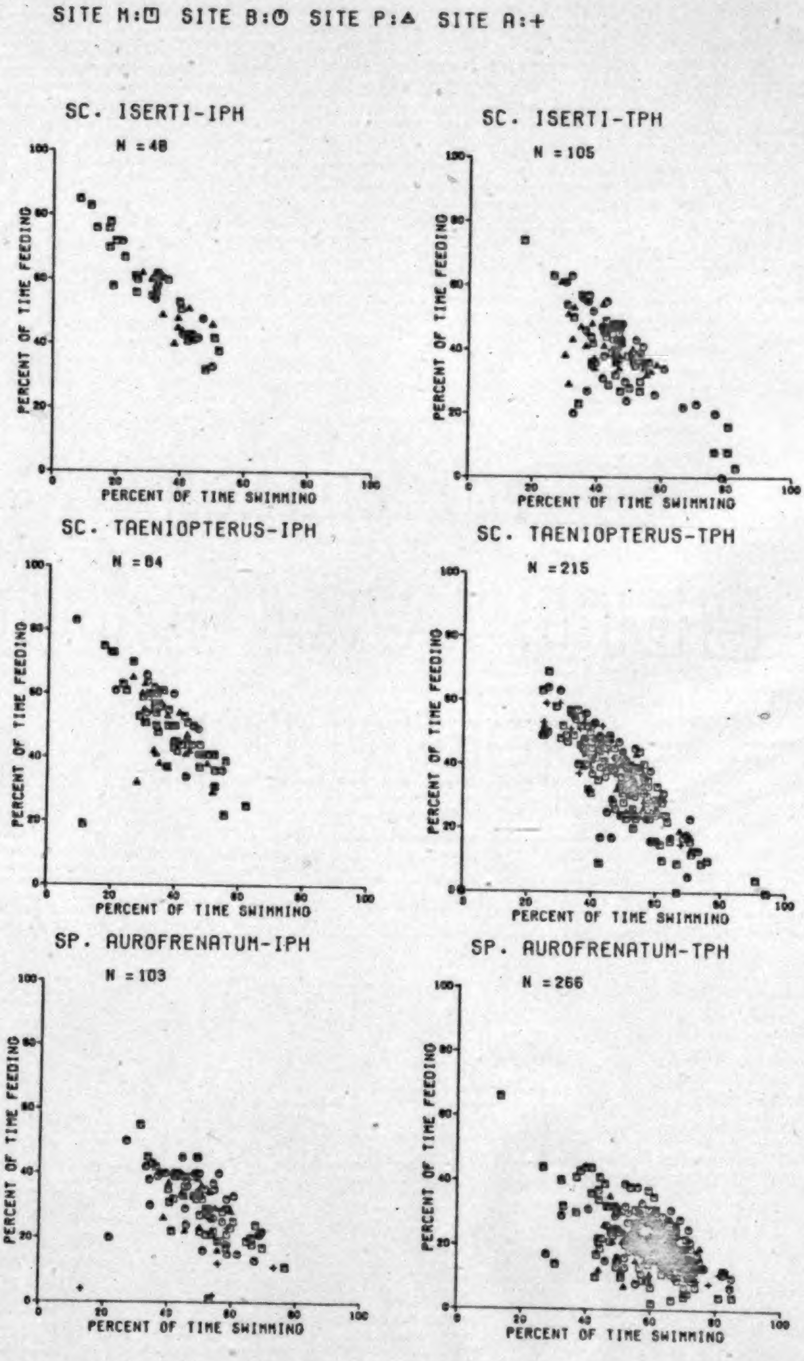


Figure 33. Percent of time spent swimming versus time spent feeding for Barbadian parrotfish



females had gonadal indices that were between 6 and 12 times those of Tph (Table 27), proportionally more than their extra feeding time. Iph fish conserved energy by using expensive aggressive behaviours less often than Tph males.

All Tph fish spent more time swimming high above the bottom than Iph, although this activity took up only 2 to 4 % of their time. High swimming by Tph could be a form of advertisement as it made the fish more conspicuous.

Sp. aurofrenatum sat motionless more than the other species, partly a result of its feeding habit of stopping momentarily between bites. All parrotfish were chased by damselfish approximately the same percent of their time (1.8 - 3.5 %). Averaged over all sites, Iph fish were more susceptible to damselfish chases than were Tph. However, this trend was less marked, or even reversed at Site M where Iph fish were not found in high damselfish areas (Chapter 5). Feeding was negatively correlated with damselfish interactions only in Tph *Sp. aurofrenatum* and *Sc. iserti* at site M. Other parrotfish either avoided high damselfish areas (all Iph) or were unaffected (Tph *Sc. taeniopterus*).

All fish spent only 1 - 2 % of their time being cleaned, and 80 - 100 % of their cleaning was carried out by fish (mostly *Gobiosoma* spp.). Tph of all species were cleaned more often by shrimp than were Iph. Iph fish spent more time under cover (1 - 3 % of their total time) than did Tph, perhaps a reflection of their greater dependence on cover for protection. Other miscellaneous activities were of

Table 27. Average gonadal indices (100 X gonad weight / body weight) of parrotfish collected in Barbados.

Species:	Mean gonad Wt. (g)	Mean body Wt. (g)	Mean G.I.	n
Sp. aurofrenatum:				
Iph	0.77	77	1.0	21
Tph	0.09	111	0.1	13
Sc. taeniopterus:				
Iph	0.71	106	0.7	25
Tph	0.16	197	0.06	20
Sc. iserti:				
Iph Female	0.71	28.4	2.0	46
Iph Male	0.33	22.1	1.1	16
Tph	0.26	71.3	0.4	4

little importance (< 1 - 2 %) in the activity budget.

I paid particular attention to aggressive behaviour (Table 28). Tph fish behaved agonistically approximately two times more often than Iph, although aggression averaged only 2 to 6 % of the total activity budget. Approximately 90 % of Tph fishes' aggression was of high intensity (i.e. chases, tailstands etc.); Iph aggression was more often of low intensity (i.e. supplanting, nips, following). Iph *Sp. aurofrenatum* were most aggressive in this respect (Table 28). My observational technique was somewhat biased as most fish were interpreted as having initiated more interactions than they received. Barlow (1975) discussed the problem of detecting aggression directed towards the animal under observation. However all Iph received more aggression than Tph; they were lower in the dominance scale.

My data revealed another apparent bias. The Iph scarids that I observed received less aggression from Tph males, as a proportion of their total activity, than Tph males meted out to Iph (see Tables 30 to 32). I may have been choosing to observe sedentary Iph that were residents and harem-mates of Tph males more often than vagile and difficult to follow transients. This suggests that Tph males interacted with extra-haremic Iph as well as their own. The Iph of all three species received attacks from their own Tph ca. 66 % of the time, and from neighbouring Tph ca. 20 % of the time. I was unable to identify the male in the remaining interactions but it was likely a known male. Intruder males occasionally

Table 28. Percent of aggression in the total activity budget, and percent directed towards Iph, Tph and other scarids, percent that was given, percent at a high level of intensity, and percent with known Tph.[1]

	Sc. iserti		*Sc. taeniopterus*		*Sp. aurofrenatum*	
	Iph	Tph	Iph	Tph	Iph	Tph
Percent of total aggression:						
with Iph	71	75	53	67	81	32
with Tph	25	13	18	25	14	61
with Other	4	12	29	8	5	7
% high	52	88	62	90	75	90
% initiated	63	94	39	90	78	94
Percent of aggression with Tph that involved known Tph:[1]						
	60	7	89	39	81	67
Percent in overall activity budget:						
Total	2.8	5.6	1.7	3.6	2.1	5.9
n	48	105	84	215	103	266

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[1] When Tph males were observed, known Tph were neighbours. In the case of Iph fish, they were both harem-mates and neighbours. Neighbours attacked Iph fish ca. 20 % of the time, the haremic Tph attacked them ca. 66 % of the time.

attacked Iph, but were observed too rarely to affect the results.

There are some hints that males interacted with their own harem mates using lower intensity behaviours than when they attacked extra-haremic Iph. While watching Iph females, I perceived that 19 to 20 % of the aggression directed towards them by Tph males was low intensity. While watching Tph males I scored only 7 to 13 % of their Iph-directed aggression as low intensity. Thus Tph males may be less aggressive towards their own harem mates than towards transient or neighbouring Iph.

Both phases of *Sp. aurofrenatum* and *Sc. iserti* spent considerably more time on aggression than *Sc. taeniopterus*. Iph of all species directed most of their attacks towards other Iph, but the Tph differed in this respect. Most (2/3 - 3/4) attacks by Tph *Scarus* were against Iph conspecifics. Tph *Sp. aurofrenatum* spent most of its time chasing other Tph, the majority of which were neighbours (Table 28). Border defence is clearly important in this species. Tph *Sc. taeniopterus* primarily chased unknown intruders. Neighbours in this species generally ignored each other. Tph *Sc. iserti* also interacted rarely with neighbours. This species was most tolerant of overlap with other males (Table 24).

I also investigated the locations of aggressive interactions with the aim of differentiating border defence from dominance-related interactions among harem mates (Table 29). I expected that dominance-related interactions would occur at all points in a territory, while border-related defence would most likely occur at the periphery.[13] I first tested whether the location of interactions directed against Iph or Tph was independent of the study site using contingency chi-square analysis. Iph-directed aggression by Tph *Sc. taeniopterus* was more often central at site M than elsewhere ($X^2(3) = 11.7$, $P < 0.01$). Iph-directed aggression by Iph *Sp. aurofrenatum* was most often peripheral at site P ($X^2(2) = 8.5$, $P < 0.025$). Otherwise there were no significant differences, so I tested whether the total number of peripheral and central interactions differed from those expected based on the average number of peripheral and central subquadrats in each area (Table 29). Tph *Sc. taeniopterus* and *Sp. aurofrenatum* had more interactions with other Tph on their borders than expected based on the number of border subquadrats. In *Sp. aurofrenatum* Iph - Tph interactions were also more common on the borders of the Tph male than expected. These interactions were not the result of Tph herding their own Iph back inside as apparently is the case for the cleaner wrasse *Labroides dimidiatus* (Robertson and Hoffman, 1977). My observations indicated that Tph *Sp. aurofrenatum* often chased Iph away from, or along their territory borders rather than back inside.

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[13] Peripheral interactions were defined as having occurred in the same subquadrat on computer maps as the Tph male's territorial limit. All other interactions that occurred inside the boundary were considered central. For Iph fish I took the position relative to an overlapping Tph's boundary. A small number of interactions at site M occurred outside any Tph boundary.

Table 29. Percent of interactions that were peripheral and central to Tph territory boundary. Chi-square test with expected values based on the average proportion of peripheral and central subquadrats at each study area are based on the raw values. Number of interactions shown in parentheses. *: $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Tph fish observed % interact with			Iph fish observed % interact with			% expected
	Iph	Tph	Other	Iph	Tph	Other	
Sp. aurofrenatum							
	(267)	(299)	(56)	(66)	(8)	(6)	
Border	58	65	52	49	88	67	50
Central	42	35	48	51	12	33	50
X^2	7.1	26.6	0.1	0.1	ND[2]	ND[2]	
P	**	***	ns	ns			
Sc. taeniopterus:							
	(394)	(141)	(46)	(41)	(16)	(17)	
Border	45	67	46	27	19	35	46
Central	55	33	54	73	81	65	54
X^2	0.1	27.2	0.0	5.8	4.6	0.7	
P	ns	***	ns	*	*	ns	
Sc. iserti:							
	(247)	(44)	(51)	(53)	(27)	(9)	
Border	62	77	76	68	33	56	70
Central	39	23	24	32	67	44	30
X^2	9.3	1.0	0.9	0.2	17.8	ND[2]	
P	**	ns	ns	ns	***		

ND[2]: Sample too small to test.

Scarus taeniopterus and *Sc. iserti* Iph - Tph interactions were more often central than peripheral to the Tph boundary, and were likely the expression of dominance by the Tph male to his harem members, or exclusion of Iph males, rather than border defence. Iph *Sc. taeniopterus* also interacted with other Iph more often than expected in the centre of their Tph's territory (Table 29).

Parrotfish interacted with other scarid species in proportion to the number of border and peripheral subquadrats in their territories. In other words, they interacted with other species when they were encountered, and did not selectively exclude them at their borders. Interspecific aggression did not result in exclusion of other species. Whether it allows the dominant species first access to food, or simply reflects general aggressive behaviour, is unknown.

I also investigated the positions of interactions involving Iph fish relative to the Iph's home range borders. In all three species, from 70 to 80 % of interactions between Iph occurred at the edges of their ranges. From 75 to 95 % of Iph - Tph aggression took place at the periphery of the Iph fish's range. Thus while the position of interactions relative to the Tph's border depended on the species (they were more often central in the *Scarus* species, and were peripheral in *Sp. aurofrenatum*), they usually occurred at the edges of the Iph's range. This could mean that Iph became more aggressive on their home range borders, and that they were more likely to be attacked there. Aggression from Tph males may serve to keep Iph harem members inside the male's borders.

Parrotfish priorities of defence

Differences among species in both the objects of their aggression, and the distribution of that aggression within the territory highlight their different priorities of defence. Tph *Sp. aurofrenatum* channel their aggressive energy into defending their borders from both Tph and Iph conspecifics. Aggression towards other Tph would be adaptive in species that defended mates as a resource (Thresher, 1979a). Many of the Iph that Tph *Sp. aurofrenatum* chased on its borders were probably extra-haremic. Some of these could have been males and thus potential rivals (Chapter 6). However, most were undoubtedly female and aggression towards them seemed anomalous. It was unlikely that Tph were excluding potential food competitors by chasing Iph females; the amount of Iph- directed aggression was unrelated to an area's food supply (Figure 4, Table 30). Sites P and A, with scarce food (Chapter 3) should have had the highest levels of Iph-directed aggression but did not. Attacks on Iph at territory borders may be directed towards neighbouring or transient Iph females. Aggression can inhibit maturation or sexual activity of subordinates (Farr, 1980; Jones and Thomson, 1980). It may also inhibit sex reversal (Robertson, 1972; 1973).

Terminal phase *Sc. iserti* allocated most of their aggression time to attacking Iph, as does the wrasse *Thalassoma bifasciatum* (Warner and Hoffman, 1980b). Both species have many Iph males, unlike *Sp. aurofrenatum* and *Sc. taeniopterus* (Warner and Downs, 1977; Robertson and Warner, 1978; Warner and Robertson, 1978; Dubin, 1981). Tph *Sc. iserti* may attack Iph fish in order to detect and exclude Iph males as well as to aggressively dominate yellowfin females. Its high feeding rates hint that *Sc. iserti* may be the most energy-limited of all the species. It may reserve its Tph-directed aggression for a brief period around spawning time (Barlow, 1975) and otherwise spend time on lower intensity and less costly dominance of Iph fish.

Terminal phase *Sc. taeniopterus* spent surprisingly little time on aggression considering the size of their territories. Three factors may account for this. First, this species has few Iph males and unlike *Sc. iserti*, Tph *Sc. taeniopterus* may be spared the task of detecting and excluding them. Second, Tph males exhibited a magnificent array of subtle colour changes, particularly when high swimming, which may have advertised or displayed to distant males. Third, this species spawned in the early morning (Dubin, 1981), unlike the others which did so at mid-day (*Sc. iserti*), or in the late afternoon (*Sp. aurofrenatum*; Table 33, Clavijo, 1980a). Aggression and intrusion levels were high very early in the morning as males returned from their night-time sleeping spots (Dubin and Baker, 1981). After re-establishing their claim to a territory, and spawning, Tph *Sc. taeniopterus* may be under less pressure than the other species to protect their borders from neighbours, exclude intruders, or dominate Iph females.

The aggression of Iph fish was primarily related to dominance of harem mates. Although some defence of the Tph's border occurred (Figures 24 to 26), it was not more frequent than expected based on the number of border subquadrats. However, aggression involving Iph was more common near the edges of their own home ranges where they were perhaps both more aggressive and more likely to be attacked.

In summary, the three species observed did proportion their time differently to each activity. The *Scarus* species fed more than *Sp. aurofrenatum* which perhaps conserved energy by remaining motionless more often. Such differences in activity budgets may facilitate the coexistence of these three species. Although they use the same space, they do not behave identically within it.

The species differed in their defence priorities, Tph *Sp. aurofrenatum* allotted most of their aggression time to excluding other Tph males on their borders. Both phases of this species also attacked Iph fish on the Tph borders. The Tph *Scarus* on the other hand, used their aggression time to dominate Iph fish within their borders. These differences may be related to the need to detect Iph males. *Sc. taeniopterus* may have to invest less energy in aggression during the day because of its early morning spawning, lack of Iph males, and extensive use of colour changes as territorial advertisement. In all species Iph-directed aggression may function to restrain Iph within their Tph's borders, and to exclude extra-haremic Iph.

Other factors affecting activity budgets: fish size, time of day, and occupancy

I wanted to test whether the factors fish size, occupancy and time of day affected a species' activity budget. Size was important because of its bearing on reproductive success and dominance status (Warner, 1975b, Waldner and Robertson, 1980a). I hypothesized that small fish, both Iph and Tph, would spend more time than large fish feeding and less time in energetically costly behaviour, like aggressive interactions, although they might be more subject to aggression from larger fish. Other species vary their activity budgets over the day, particularly near dawn and dusk (Dubin and Baker, 1981; Nursall, 1981). I could not investigate such differences because activity budgets were generally measured 3 and 11 hours after sunrise. Nevertheless, I was interested to learn whether allocation of time to behaviours remained stable over the rest of the day. In a few Tph *Sp. aurofrenatum* and *Sc. taeniopterus* for which the arrival times in their territories were known accurately, I investigated whether behaviour changed over the course of their occupancy.

There were few effects of fish size class on activity budgets (Anova). Large (> 165 mm SL) Tph *Sp. aurofrenatum* at site M sat more than smaller fish. Their size range was too slight at the other sites (Chapter 6) to test for differences. Hoffman and Stouder (1980) reported that small Tph *Sp. aurofrenatum* in Panama fed more rapidly than large males, but this was not the case in Barbados.

Small Iph *Sp. aurofrenatum* (< 120 mm SL) swam less and fed more, but the same trend was not apparent in Iph of other species. Small (< 125 mm SL) Iph *Sc. taeniopterus* received more aggression from other Iph. Small (< 190 mm SL) Tph *Sc. taeniopterus* also swam less and fed more than larger fish. So some small fish behaved in accordance with my predictions but most did not.

Time budgets also varied little over the day.[14] At site M, Tph *Sp. aurofrenatum* swam least and fed most in the morning, but showed the reverse trend at site B. Tph *Sc. iserti* at site P, and Iph at site B, also swam most and fed least in the morning. Iph *Sc. taeniopterus* had most interactions with damselfish in the morning. Iph *Sc. iserti* at site M interacted least with Iph, but swam most and fed least at mid-day.

There are few patterns to these diurnal time budget changes. The blenny *Ophioblennius atlanticus* fed least in the morning when it was often spawning (Nursall, 1981). The author suggested that such diurnal cycles in feeding might reduce competition with other herbivorous species. This does not appear to be the case for scarids. Parrotfish in the Virgin Islands had low feeding rates in the early morning

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[14] Time periods were morning (3 to 5 h after sunrise), noon (6 to 8 h) and afternoon (9 or more h).

(Sartori and Bright, 1973). The food source of parrotfish, benthic algae, may vary in quality or abundance throughout the day (C.M. Hawkins, pers. comm.), and parrotfish may allocate their feeding time to reflect this. However, activity budgets of the species studied here showed little change over the time span investigated.

I tested the effects of occupancy time of Tph *Sc. taeniopterus* and *Sp. aurofrenatum* by correlating occupancy in days with percent of time spent in each activity. If a correlation was significant I then looked at individuals that were repeatedly sampled during the study to see if their behaviour fit the trend shown by the correlation.

There were no effects of occupancy discernible for established *Sc. taeniopterus* except that fish with longer occupancies swam more at site M ($r = 0.68$, $P < 0.05$, $n = 11$). However, *Sc. taeniopterus* transforming from Iph to Tph colours at all sites did change their activity budgets over two months. The time spent swimming increased ($r = 0.42$, $P < 0.05$, $n = 17$), while cleaning decreased ($r = -0.51$, $P < 0.05$). Perhaps the early stages of sex or colour change cause some discomfort and induce fish to solict more cleaning. Aggression directed towards other Iph increased ($r = 0.49$, $P < 0.05$), but seemed to level out after a month. Thus new Tph males, besides shifting apart over time, invested more time in interactions with Iph conspecifics. There were no trends due to duration of occupancy in Tph *Sp. aurofrenatum*.

Scarids and labrids adjust their behaviour rapidly to new situations (Jones, in press; Warner, pers. comm.). For example, intruder males shift from sneaking through territories to openly displaying within minutes of finding an empty space. Their behaviour is indistinguishable from that of long-term residents after several days. Early in their occupancy newly arrived males spent a greater amount of time interacting with both intruder and neighbour males, but this declined rapidly as they became established (Dubin, in prep.). Newly arrived Tph spawned on their first day in a territory at the offshore sites. A change in social status (e.g. from intruder to resident Tph, or from Iph to Tph male) engenders behavioural changes that occur over a short span of time, after which behaviour remains stable.

In summary, fish size, time of day and duration of occupancy had few effects on activity budgets. Some small fish conserved energy by swimming less and feeding more. A few species varied their feeding over the day with the least occurring in the morning. Changes in behaviour due to occupancy occurred relatively rapidly in the two groups investigated, and were related to changes in social status. Scarids are capable of short-term behavioural transformations when the situation is favourable.

Activity budget differences between sites

In order to determine how parrotfish responded to differing ecological conditions at each study area, and what behavioural differences could account for harems and permanent territories offshore (sites A, B, P) but non-haremic, temporary territories inshore (site M), I subjected the activity budgets of each species and phase to analyses of variance for differences between study sites (Tables 30 to 32). Duncan's multiple range tests were used to interpret any significant differences found. The percent of time spent in submission was not normally distributed and was tested for Iph only using the non-parametric Kruskal-Wallis Anova (Siegel, 1956). It occurred too rarely in Tph males to be tested. In all three species, Iph fish performed more submissive gestures at the offshore sites than inshore although the difference was not quite significant. When data for sites B and P were lumped the differences were significant[15], indicating that Iph fish offshore did indeed spend more time behaving submissively.

The activity budget at each site for both Iph and Tph *Sp. aurofrenatum* is presented in Table 30. Results from two patch reefs in Panama are also presented although these were not included in the analysis of variance. Iph fish at site M sat and were chased by damselfish more than elsewhere. Two apparent differences were a result of small sample size at site A; the five Iph fish were observed there late in the afternoon, and fed less but sat under cover more than elsewhere.

Both Iph and Tph fish in Panama spent considerably less time feeding than in Barbados. In Panama, they ate mostly

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[15] *Sc. iserti* $X^2(1) = 4.3$; *Sc. taeniopterus* $X^2(1) = 4.5$; *Sp. aurofrenatum* $X^2(1) = 5.8$; $P < 0.005$ in all cases.

Table 30. Average activity budget at each site for Iph and Tph *Sp. aurofrenatum*. Results from analysis of variance and trends in significant differences among sites are shown. Values may not sum to 100 % due to round-off errors. Data from Panamanian population were not included in Anova. (Sample size-minutes of observation). Trend shows which sites were significantly different based on Duncan's Multiple Range Tests. Sites that do not appear in a trend were signficantly different from neither group. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.
Dams.: damselfish. Subm.: submission. Misc.: miscellaneous. Other: other scarid species.

	Behaviour (% time spent in each activity):								
	Swim	Feed	Sit	Interact with				Subm.	Misc.
				Dams.	Iph	Tph	Other		
Sp. aurofrenatum Iph									
Site M (38-399)	51.4	28.8	8.5	3.8	2.1	0.1	0.1	0.1	5.1
Site A (5-63)	51.2	10.6	8.2	2.5	0.1	0.0	0.0	0.0	27.1
Site B (48-418)	50.1	32.2	4.5	1.5	1.5	0.5	0.02	0.5	9.3
Site P (12-104)	51.2	29.6	4.6	3.0	2.0	0.3	0.2	0.4	8.8
Panama (24-260)	65.2	20.1	7.8	1.1	1.1	0.03	0.2	0.3	4.9
F(3,99)		7.9	5.7	5.5					8.7
P		***	**	**					***
Trend		A<M,P,B	B,P<M	B<M					M,P,B<A
Sp. aurofrenatum Tph									
Site M (79-711)	55.6	23.0	6.9	3.8	0.5	3.0	0.2	0.1	6.9
Site A (16-325)	68.8	15.5	6.0	2.3	1.1	1.4	0.8	0.0	4.1
Site B (136-1644)	62.4	21.1	2.4	1.0	2.7	3.6	0.6	0.0	6.2
Site P (35-510)	59.0	20.9	2.9	1.4	2.3	5.8	0.2	0.0	7.5
Panama (17-345)	69.1	13.9	4.3	1.3	0.9	1.1	1.1	0.0	8.4
F(3,262)	11.0	3.5	22.7	16.0	12.2	3.2	3.0		
P	***	*	***	***	***	*	*		
Trend	M,P<A	A<P,B,M	B,P<A,M	B,P<M	M,A<B M<P	A,M,B<P	P,M<A		

seagrass (60 - 85 %) and much less dead coral or sand than in Barbados. Seagrass may be a richer food source than microphytic algae.

Tph *Sp. aurofrenatum* in Barbados differed in their activity budgets between areas. The Tph of Site A swam more and fed less than elsewhere. This did not imply that they expended more energy; most of the Site A males, which were larger than elsewhere (Table 22), moved more slowly through the water than males elsewhere, gliding between pectoral fin flaps. Site A and site M Tph showed some similarities, and sat and were chased by damselfish more than on the barrier reef. Males invested differing amounts of time in aggression. Barrier reef Tph attacked Iph more than at site M, while site A was intermediate. Site P Tph had more aggressive interactions with Tph males than elsewhere, perhaps a reflection of the high rates of intrusion there (see Figure 14). Tph chased other parrotfish (solitary Iph *Sp. viride*) most frequently at site A.

Besides feeding less, Panamanian Tph swam more than their Barbadian counterparts. They invested comparatively little time in conspecific interactions, but a good deal more in chasing other species, primarily Iph *Sp. chrysopterum* and *Sp. rubripinne*. This was due in part to the geometry of the reefs in Panama. Each roughly circular patch reef was ringed by Tph *Sp. aurofrenatum* territories, much like beads on a necklace. Each Tph had only two conspecific neighbours with which to interact, unlike Barbadian Tph who were surrounded by Tph (except at Site M). Panamanian territories faced sea grass beds surrounding each patch reef where the other *Sparisoma* species were abundant (Robertson and Warner, 1978), and most interspecific aggression by Tph was of low intensity.

At site M, Iph and Tph *Sc. taeniopterus* also sat and were chased more often by damselfish (Table 31). Iph-directed aggression was more common offshore than at Site M. Again, Site A was intermediate. Iph fish interacted with both Iph and Tph most at site P. Unlike Tph *Sp. aurofrenatum*, Tph *Sc. taeniopterus* spent the most time feeding at site A, and more at site B than at Site M.

Initial phase *Sc. iserti* at site M spent the most time feeding and the least time swimming (Table 32). Only Tph were chased by damselfish more there than at the other sites; the trend for Iph fish was similar but was not quite significant ($P < 0.1$). Tph were aggressive to Iph more often offshore than at Site M, and the difference between Site B and Site P was also significant.

Certain differences in activity budgets could be related to the density of damselfish. All parrotfish were chased most often by damselfish at site M and next most often at site A, where damselfish densities were high (Chapter 3). Both *Sc. taeniopterus* and *Sp. aurofrenatum* spent more time sitting at these two sites. By remaining motionless, they perhaps elicted less aggression from damselfish. Bluegill sunfish soon habituated to stationary

Table 31. Average activity budget at each site for Iph and Tph *Sc. taeniopterus*. Results from analysis of variance and trends in significant differences among sites are shown. Values may not sum to 100 % due to round-off errors. (Sample size- minutes of observation). *: P < 0.05; **: P < 0.01; ***: P < 0.001. See Table 30 for explanation.

	Behaviour (% time spent in each activity):								
				Interact with					
	Swim	Feed	Sit	Dams.	Iph	Tph	Other	Subm.	Misc.
Sc. taeniopterus Iph									
Site M (48-468)	38.2	49.9	2.2	4.9	0.6	0.1	0.5	0.01	3.7
Site B (17-168)	36.4	55.0	0.7	0.8	1.1	0.3	0.4	0.1	4.4
Site P (19-165)	38.4	47.1	1.5	2.7	1.6	1.1	0.4	0.3	6.9
F(2,81)			3.1	12.7	3.2	5.0			
P			*	***	*	**			***
Trend			B<M	B,P<M	M<P	M,B<P			
Sc. taeniopterus Tph									
Site M (89-781)	49.8	33.8	4.1	4.8	0.8	0.5	0.4	0.01	5.7
Site A (22-423)	43.5	43.9	2.2	3.0	1.1	1.2	0.1	0.0	5.2
Site B (80-1153)	48.6	38.3	1.3	1.1	3.9	1.3	0.1	0.0	5.4
Site P (24-398)	52.5	34.8	1.4	1.9	4.1	0.8	0.4	0.0	4.0
F(3,211)		4.2	9.7	32.4	14.8		3.8		
P		**	***		***		*		
Trend		M,P<A	B,P,A<M	B,P<M	M,A<B,P		A<P		

Table 32. Average activity budget at each site for Iph and Tph *Sc. iserti*. Results from analysis of variance and trends in significant differences among sites are shown. Values may not sum to 100 % due to round-off errors. (Sample size-minutes of observation). *: P < 0.05; **: P < 0.01; ***: P < 0.001. See Table 30 for explanation.

	Behaviour (% time spent in each activity):								
	Swim	Feed	Sit	Interact with				Subm.	Misc.
				Dams.	Iph	Tph	Other		
Sc. iserti	Iph								
Site M (22-203)	28.7	61.4	0.6	2.6	1.9	0.6	0.1	0.1	4.1
Site B (13-233)	37.3	52.6	0.6	1.6	1.7	0.8	0.3	0.5	4.6
Site P (13-125)	37.3	52.2	0.2	1.5	2.4	1.0	0.1	0.3	5.1
F(2,45)	4.1	3.3							
P	*	*							
Trend	M<B,P	P,B<M							
Sc. iserti	Tph								
Site M (33-318)	47.4	38.9	1.0	3.8	1.3	0.5	0.6	0.0	6.6
Site B (39-430)	47.9	39.2	1.1	0.6	4.1	1.0	1.3	0.01	5.3
Site P (33-349)	42.5	43.5	0.7	0.8	7.2	0.5	0.8	0.02	4.1
F(2,102)				39.9	10.6				
P				***	***				
Trend				B,P<M	M<B<P				

dummies but continued to respond to moving ones (Colgan and Gross, 1977). *E. planifrons* allowed stationary (i.e. anaesthetized) heterospecific intruders to enter further into their territories than normal motile ones (Thresher, 1976b). Isolated individuals remaining immobile, and numerous ones forming large feeding schools, may be two alternate strategies used by parrotfish to overcome the aggression of territorial damselfish.

Interactions with Iph fish appeared to separate site M from the others. Tph of all species were aggressive to Iph fish least often at site M. Iph-directed aggression was generally lower at site A than on the barrier reef sites B and P, but it always exceeded the amount seen at site M. Fish density (see Table 5) had no relation to the amounts of time spent on aggression at any site. Observations on the locations of Iph-directed aggression hinted that males excluded extra-haremic Iph and confined haremic Iph within their borders. Since most males at site M lacked harems, this behaviour was less common.

In summary, variations between sites in activity budgets reflected two factors: overcoming damselfish aggression in high density areas, and maintaining a harem. Otherwise fish varied little from site to site in their activity budgets.

Feeding behaviour

Parrotfish did not appear to compete interspecifically in Barbados to the point of partitioning space (Chapter 5).

Nor did any species appear to be much affected by differing food levels. Conspecifics showed few significant differences between sites in the amounts of time allocated to feeding (Tables 30 to 32). Iph *Sc. iserti* spent more time feeding inshore at Site M. *Sp. aurofrenatum* fed least at site A (although low values for Iph there may have been artifacts of small sample size). *Sc. taeniopterus* fed the most there

In order to test whether a species grazed on different items at different sites, and whether the species present in one area showed feeding specializations which might reduce interspecific competition for food, I analysed the percent of bites made on various substrates at each site[16] for 10 Iph and 10 Tph fish (Figure 34). The data were arcsine transformed to improve their normality (Sokal and Rohlf, 1969). I first tested whether Iph and Tph conspecifics differed in the percentage of bites on each of six substrate categories: sand, coral rubble, dead areas of coral heads, the dead bases of branching corals (i.e. staghorn and finger corals), sponges and other substrates (primarily gorgonians and the tips of sea urchin spines). Only two differences between phases were significant: *Sc. iserti* feeding on sand (Tph exceeded Iph), and *Sc. taeniopterus* feeding on other substrates (Iph exceeded Tph). Therefore I combined the information for Iph and Tph. To determine whether species had differing food habits, and whether site affected what substrate they grazed, I performed a two-way analysis of

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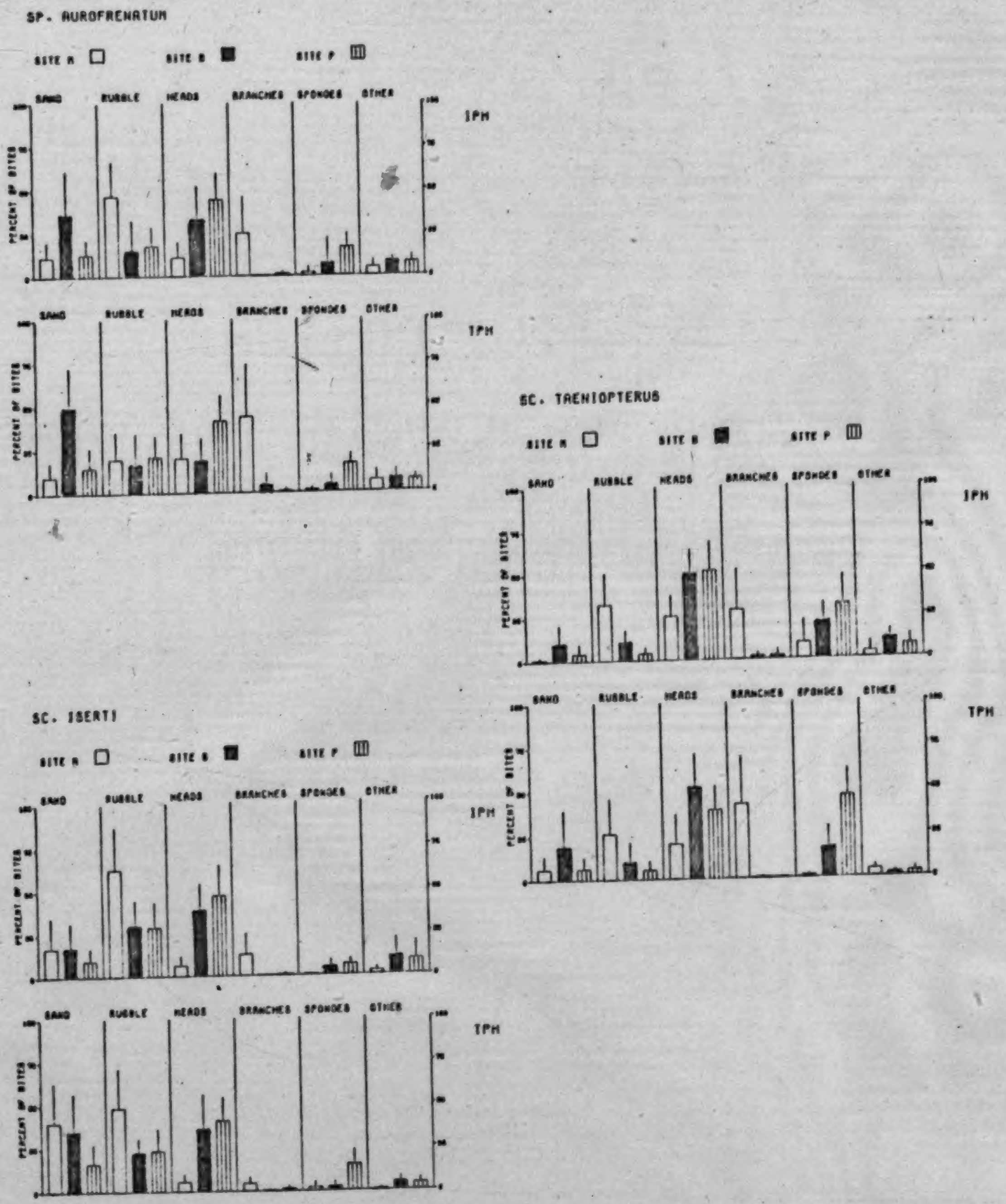
[16] No such observations were made at Site A due to time limitations.

Figure 34. The percent of bites made on different substrates by 10 Iph and 10 Tph parrotfish at each study site during a 5-minute observation period. Values are mean ± 95 % confidence interval. Branches are staghorn and finger corals; heads are dead sections of coral heads.



variance for each substrate category (site by species). In all cases there was a significant effect due to site; species' feeding habits changed depending on where they resided. Species also showed significant differences in the amounts of grazing on all food categories except "other", but they did not differ in the same way at all sites (i.e. the interaction terms were significant) for feeding on sand, branched corals and sponges. In other words, no species was locked into an inflexible preference for any substrate category. Rather, they appeared to feed in relation to a substrate's abundance: branching corals and rubble were grazed most at Site M where they were most abundant (Chapter 3); coral heads were most often grazed at the barrier reef, and sand was often grazed at Site B by all but *Sc. iserti*.

Overlap indices (Horn, 1966) calculated between pairs of species were higher for different species at the same site (O.I. = 0.78 ± 0.07 (S.D.), n = 36) than for conspecifics at different sites (O.I. = 0.60 ± 0.11, n = 18; t(52) = 3.0, P < 0.01). The feeding habits of different species at the same site had more in common than those of the same species in different environments; parrotfish were altering their feeding patterns to graze what was available, and all species made the same alterations. Some interspecific differences were noted, but they were slight. *Sc. taeniopterus* grazed sponges more than the other species, *Sc. iserti* was generally the heaviest grazer on sand and rubble. *Sp. viride* grazes sand least of Barbadian scarids

(Frydl and Stearn, 1978; Scoffin et al; 1980). Randall's (1967) study on stomach contents showed that the species studied here were ingesting the same algae, while others (e.g *Sp. rubripinne, Sp. chrysopterum*) ate more sea grass.

Jones (1968) was able to separate 20 species of Pacific acanthurids into groups based on their gut morphologies, stomach contents and spatial distributions, but concluded that food was not limiting. Bakus (1967) estimated that algae was more than sufficient in quantity at Eniwetok Atoll to support herbivore populations there. While Choat and Robertson (1975) reported some differences in feeding among scarids in Australia, a complete separation of the 18 species they studied according to feeding habits was not made. Parrotfish cluster into groups of species that have similar resource requirements, yet compete interspecifically very little. The group I concentrated on: *Sp. aurofrenatum, Sc. iserti* and *Sc. taeniopterus*, appears to be such a one; its members share both the same space and the same food. While differing dental morphologies (Schultz, 1958), and feeding behaviours may reduce competition between *Sparisoma* and *Scarus*, there are few indications of feeding specializations in these species. Competition for food does not play a large role in parrotfish behaviour.

Food supply differences between sites M, B and P did not affect parrotfish feeding rates; there were no significant differences between sites in the number of bites per minute for any species (Kruskal-Wallis Anova). This contradicted my earlier hypothesis (Chapter 3) that rates should be lowest at site M where damselfish might disrupt feeding. However, feeding rates of *Sc. taeniopterus*, and Tph *Sc. iserti* were more variable at Site M than elsewhere (F Test; Snedecor and Cochrane, 1980). This suggests that either habitat heterogeneity (e.g in damselfish densities or locations of grazing substrate) or differences among the fish were responsible. Size affected feeding rarely, so the former explanation may be more likely.

Food supply differences in Barbados were not responsible for the behavioural differences between study areas. However, greater food abundance or quality was perhaps responsible for the low feeding rates of *Sp. aurofrenatum* in Panama. Frydl and Stearn (1978) reported that Barbadian parrotfish had more indigestible inorganic matter in their guts than those feeding in Virgin Islands sea grass beds. They suggested that Barbadian scarids compensated for lower quality food by increased gut turnover rates. Panamanian *Sp. aurofrenatum*, which ate mostly sea grass, spawned every day (S.G. Hoffman, pers. comm.) but did not in Barbados. Territories were also larger in Panama. Thus relatively large differences in food supply could affect the amounts of time that parrotfish allocate to social interactions, spatial defence or spawning.

Reproduction

The information presented above suggests that parrotfish competed interspecifically neither for food nor for space, and that the type of coral cover, the abundance of food, and the density of damselfish competitors had few effects on social interactions. Most of the differences in social organization between study areas could, in fact, be related to reproductive activity. Parrotfish inshore at site M spawned rarely. They did so regularly offshore (Table 33). Site P was the favoured location for group spawning by Iph (and some Tph) *Sc. iserti*. Large groups congregated on its northeast slope and were seen nearly every day. Pair spawning by *Sc. taeniopterus* and *Sp. aurofrenatum* was also most common there.

Each species had specific spawning times at the offshore sites (Table 33). Spawning inshore seemed to be a chance event, unlike the more predictable synchrony of reproductive activities offshore. Spawning was seen in all months of the year, and at all phases of the moon, although not every day.

Fish collected inshore at site M were not sexually inactive (histological criteria of Warner, 1975a). Tph males had full sperm ducts and Iph females showed active vitellogenesis. Some of both sexes showed signs of recent spawning. Given the relatively low costs of producing sperm, Tph males may always keep ripe sperm on hand, even when their immediate mating prospects are dim. The fact that intruder males spawned on their first day in a vacated territory indicates that males may be always prepared to spawn. The rarity of spawning at site M, and the transience

Table 33. Number of days on which spawning and courting was observed per 100 hours observation, time during each species' spawning period, and earliest and latest times of day that reproductive activities were observed.

	Site M	Site A	Site B	Site P
Sp. aurofrenatum:				
Pair spawn	22.4	38.5	41.0	48.5
Earliest-	1200-	1650-	1610-	1610-
Latest (hours)	1740	1807	1745	1825
Sc. taeniopterus:				
Pair spawn	8.1	58.8	75.0	93.0
Earliest-	1035	0558-	0700-	0634
Latest (hours)		0748	1005	1035
Sc. iserti:				
Pair spawn	2.1	ND	8.8	8.2
Group spawn	0.7	ND	6.6	15.5
Earliest-	1550-	ND	1100-	1340-
Latest (hours)	1645	ND	1705	1700

of much of its population hint that parrotfish were exploiting the abundant food inshore, and migrating elsewhere, probably offshore, to spawn.

F. Summary and discussion

High densities of the damselfish *E. planifrons* do affect parrotfish behaviours: many sat and were chased more by damselfish at sites A and M. However, these differences did not account for variability in social structures. A low frequency of interactions between Iph and Tph fish of all three species did separate site M from the others. Iph-directed aggression may be central to formation of a harem. The actual mechanism by which it works is unknown. Jones (in press) found that Tph male *Pseudolabrus celidotus* which interacted aggressively more often with Iph females had greater spawning success. Tph of all species were not herding Iph fish back inside their borders as does *Labroides dimidiatus* (Robertson and Hoffman, 1977). High levels of aggression against Iph fish that are on a Tph male's border may teach Iph residents, by negative reinforcement, to avoid borders, so that they remain within their Tph's territory. A study on the levels of aggression against Iph fish at different distances from the Tph territorial border using Iph dummies or the model-bottle technique (Myrberg and Thresher, 1974) would be very useful in determining how proximity to a border affects responses to Iph. It would be even more interesting to present Tph males with Iph fish from their own, neighbouring, and strange harems (e.g.Thresher, 1976b) in order to test whether Tph respond differently to familiar and unfamiliar Iph. It is possible that Tph males behave more aggressively to neighbouring or strange Iph, than to their own.

The difference between sites in time allocated to Tph aggression is not so clearly related to harem formation. Aggression levels were relatively high at site M in *Sp. aurofrenatum* probably because the temporary males were always establishing new borders. Intrusions by unknown Tph may have increased the amount of Tph-Tph aggression at the offshore sites.

Species did not show clear preferences for particular grazing substrates. Overlap in food was high, particularly between fish-inhabiting the same locations. Parrotfish showed flexibility in feeding, and did not appear to compete interspecifically for food.

Spawning occurs rarely inshore, but regularly offshore. The differences between inshore and offshore areas in social systems appear to reflect these differences in reproductive activity. Lack of Iph harems, loose packing of space, transient populations and little competition for territories there can all be related to the fact that this inshore area was a sub-optimal location for broadcasting eggs.

VIII. General discussion

Parrotfish social organization clearly varies between reef areas. In this section I will discuss what ecologial factors may be responsible for such differences, and how each species copes with its complex and variable environment. My results will be considered in the light of recent arguments on how reef communities are structured (e.g. Sale, 1978b; Smith, 1978). I will also consider how social systems contribute to population stability, and suggest some avenues for future research.

Differences in ecological variables and in parrotfish social systems between study sites are summarized in Table 34. At offshore areas in Barbados, Tph male parrotfish formed a mosaic of contiguous, permanent territories that were much in demand. Iph fish lived in size-dependent dominance hierarchies there as members of a harem. Fish spawned regularly. At one inshore location, a radically different pattern was seen, with *Sp. aurofrenatum* departing most from the haremic system, and *Sc. taeniopterus* the least. Inshore, Tph male *Sp. aurofrenatum* held shifting territories for only a few weeks, and harems were not formed. The situation was very similar in *Sc. iserti*, although a few males appeared to be intermittent residents for up to a year. While some *Sc. taeniopterus* males were long-term residents that perhaps had harems, others remained temporarily, and lacked harems. Several common threads ran through the social systems of all three species living

Table 34. Summary of differences between study areas in ecological variables and parrotfish social systems.

	Site M	Site A	Site B	Site P
Ecological variables:				
Food:				
Supply	High	Low	Moderate	Low
Distribution	Patchy	Patchy	Even	Even
Coral cover:	Staghorn finger & rubble	Staghorn finger & rubble	Scattered heads & sand	Scattered heads & sand
Damselfish density:	High	High	Low	Low
Spawning suitability:	Poor	Good	Good	Good
Social systems:				
Presence of harems:	None [1]	Yes [2]	Yes	Yes
Type of Tph territoriality:	Temporary, shifting[1]	Permanent, probably [2]	Permanent	Permanent
Frequency of intruder Tph:	Rare	Common [2]	Common	Common
Spawning frequency:	Rare	Regular [2]	Regular	Regular

[1] Some Tph *Sc. taeniopterus* are permanent and may possess harems.

[2] No data for *Sc. iserti*.

inshore: space was not at a premium, and spawning occurred rarely.

Spawning site suitability, measured in terms of proximity to offshore waters, reef slopes and larvae-retaining gyres, appears to account for these differences. Harems, permanent territories and wandering intruders were found where spawning occurred regularly. They were not restricted to areas with particular coral cover. Parrotfish at site A, which had branching corals, and at sites B and P, which had hemispherical coral heads, had similar social systems. Likewise, the temporary, shifting territories at site M were found over branching corals, small knob-like coral heads, and rubble. While reef structure may affect the configuration of territories - adjoining territories of *Sp. aurofrenatum* formed a ring around patch reefs in Panama - it does not alter the basic plan of permanent territoriality and harems. Parrotfish do not defend shelter sites. They require coral shelter overnight, yet their territoriality breaks down before sunset while cover-seeking occurs (Dubin and Baker, 1981).

Damselfish, primarily *Eupomacentrus planifrons*, were not responsible for the differences between inshore and offshore areas. Their densities were high at two areas with different social systems (Table 34). Their territoriality and ability to exclude Iph fish may have been stronger inshore, thus preventing Tph males from maintaining harems in zones with numerous damselfish. Yet males still occupied such zones, rather than move into lower density areas where harems were also lacking. While fish dwelling over areas with many *E. planifrons* at both sites showed some behavioural similarities, such as spending more time sitting and being chased by damselfish, these behaviours did not play a central role in harem formation or permanent territoriality.

The effects of damselfish aggression on feeding seemed to be slight. Only Tph *Sp. aurofrenatum* and Tph *Sc. iserti* spent less time feeding when attacked often by damselfish. The alliances formed by both species may serve to overcome damselfish aggression. Feeding rates at site M, while sometimes more variable, were not consistently lower than elsewhere. Some solitary parrotfish, particularly Tph *Sc. taeniopterus*, Tph *Sp. aurofrenatum*, Iph *Sc. vetula*, and Iph *Sp. viride*, would feed without interruption for extended periods of time on damselfish algal mats. Sitting still may "dupe" damselfish and allow parrotfish to feed within their territories. Judging from the number of parrotfish that held space in areas with high damselfish densities, the rewards of occasional feeding on their algal lawns must exceed the nuisance of their attacks.

My results show that territoriality by Tph parrotfish does not function primarily to defend a food supply, although parrotfish obviously must meet their nutritional requirements within their territory borders. Except in *Sc. iserti*, the effect of fish size and food supply on home range size was not consistent with that expected for feeding territories. Intruders were least common at the site where food was most abundant, yet they vied for space in areas with less food (Table 34). Some parrotfish at site M perhaps responded to patchily distributed food by using space intensively, but this should not have prevented Iph and Tph individuals from overlapping in space, i.e. from forming harems.

Obtaining food was nevertheless important, particularly for the temporary populations at site M. Loose, heterospecific feeding associations were most common there. Many of the Iph *Scarus* collected inshore showed signs of recent spawning, and perhaps migrated regularly to spawn offshore, returning inshore to feed (Randall and Randall, 1963; Barlow, 1975; Colin, 1978). Small Tph males, incapable of holding territories offshore, may exploit the abundant food levels inshore where they can grow rapidly and reach more competitive sizes. Other larger males may be forced there after losing their territories elsewhere. Tph *Sc. iserti* in Panama which lack spawning territories invest their time in growth and feeding (Robertson et al., 1976; Warner and Downs, 1977). Jones (in press) noted that Tph *Pseudolabrus celidotus* switched between temporary territories inshore and intruder-like behaviour in deeper, more favourable spawning locations. Fish at site M behaved similarly, exploiting the abundant food inshore only long enough to recover their strength, replenish spent gonads, or grow to a competitive size.

Robertson and Warner (1978) may be quite correct in stating that permanent territoriality is possible in scarids only because benthic algae are a predictable and defensible resource. Obviously, if food becomes too scarce, territoriality will not be economically feasible (e.g. Carpenter and MacMillen, 1976). At the natural levels encountered in this study, food could not explain the switch between haremic systems offshore, and non-haremic ones inshore. However, it may affect certain non-critical parameters of social organization. Tph males may expand their territories if rich food is added perhaps in order to increase their harem size (Hoffman and Stouder, 1980). It will be especially important to look at parrotfish behaviour on deeper reefs where food may be scarce, and at offshore, shallow areas where both high levels of food and good spawning sites are present.

How parrotfish themselves determine an area's suitability as a spawning site is unknown. They can perhaps sense oceanic waters and currents. Tradition may also play a role. Some spawning locations persist over long periods of time (e.g. Colin and Clavijo, 1978). Proximity to reef slopes appears to be a factor as well. At site M, the few Tph males inhabiting the offshore slope (Figure 3) had the longest durations of occupancy, and performed over 50 % of the spawnings. Water movements near reef slopes may be conducive to lifting eggs off the reef. Whether females or males choose prime spawning areas (e.g. Jones, in press) is unknown. The active role that Iph play in soliciting and initiating the spawning leap hints that they make such choices. The existence of wandering, ripe Iph *Sp. aurofrenatum* offshore, and of border defence by all Iph females, suggests that competition among Iph females for space does occur. Buckman and Ogden (1973) reported that surplus yellowfin *Sc. iserti* rapidly refilled vacated territories.

Thresher (1979a) suggested that male *Halichoeres maculipinna* defended Iph females as a resource. Male parrotfish may behave similarly. At the offshore sites, intruders were more common, and residents' territories were smaller where Iph densities were higher. It is difficult to separate cause and effect here, but Tph males may expand their territories where females are less abundant in order to gain more mates.

The probability that an Iph fish is female may increase its value as a defensible resource. Thus, in *Sp. aurofrenatum* where Iph males are rare (Robertson and Warner, 1978), Tph males have a very high commitment to border defence. Tph *Sc. iserti* face the problem of Iph populations sullied by numerous 1° males. This may make Iph females less defensible, and may account for the tolerance of Tph males for overlap with others. Energetic constraints may also be operative in this species. *Sc. taeniopterus*, with fewer 1° males than *Sc. iserti*, is intermediate. Unlike its congener, Tph *Sc. taeniopterus* allowed little overlap with other males and actively defended their borders, but spent less time chasing males than Tph *Sp. aurofrenatum*.

The connection between social system and sexual structure of a species is still not completely clear. Certain of my results support the hypotheses of Robertson and Warner (1978). For example, *Sc. iserti*, the most abundant scarid, has the most 1° males, in accord with Warner and Hoffman's (1980a, 1980b) predicted effects of population size on Iph male success. Also, *Sp. aurofrenatum* males ranged more widely in size at site M, where the social system was looser. However, my results do not support Robertson and Hoffman's (1977) view that sexual dichromatism is primarily a result of male-female interactions. Males of all three species intensified their colours during interactions with other males, yet were sometimes dull-coloured during spawning. I expect that their bright colours can have multiple functions.

A haremic social system does not always result in monandry (see also Thresher, 1979a). The three species studied here had basically similar haremic systems offshore, yet one had numerous Iph males, one had moderate numbers, and one had almost none. Monandric, strongly haremic species (e.g. *Labroides dimidiatus* or *Scarus niger*) and diandric lekking ones (e.g.*Thalassoma bifasciatum* or *Scarus fasciatus* - Robertson, 1972; Choat and Robertson, 1975; Warner and Robertson, 1978) are extremes along a continuum with much room for variation in between. These authors are no doubt correct about what happens at either end of the series, but we require much more information about the middle regions.

My results do not support earlier arguments that different food sources or feeding strategies account for social behaviour differences between *Scarus* and *Sparisoma* (e.g. Itzkowitz, 1974; Barlow, 1975). Although *Scarus* fed more rapidly, and in a different fashion than *Sp. aurofrenatum*, they grazed the same substrates. Despite these feeding differences, all three species studied here had similar social organizations offshore. Iph *Sp. aurofrenatum* were more solitary than the other species, but this could reflect its lower population size rather than a different distribution of food. Iph *Sc. taeniopterus* were most solitary at site P where they were least abundant, and the same trend held for *Sc. iserti* at site A (Table 5, Appendix 1F). Other *Sparisoma* species (e.g. large *Sp. viride, Sp. rubripinne*) regularly form groups.

That males defend space primarily for spawning purposes explains in part why several species can coexist peacefully. Each species' aggression is directed towards conspecifics, most of which are harem-mates or competitors for mates rather than for food or shelter. Besides the obvious advantages of remaining on familiar ground, fish probably stay on their territories on a full-time basis because of the immense threat from intruders, ready to immediately fill vacated territories. I became aware of these costs in early

1977 after I inadvertently deprived several Tph *Sp. aurofrenatum* residents of their territories by holding them in traps for several hours. Despite violent battles with the intruders that had claimed their territories in the meantime, they failed to regain them on release. Space for shelter or obtaining food, while it must eventually limit parrotfish populations, may not be saturated on reefs (Robertson and Sheldon, 1979; Robertson et al., 1980).

Differences in spawning times and site attachment may explain why the three species studied here did not respond in identical ways to the environmental factors at each site. *Sc. taeniopterus* varied least between inshore and offshore areas. In Barbados, the *Scarus* species migrate regularly to night-time sleeping spots, while *Sp. aurofrenatum* does not (Dubin and Baker, 1981). Since *Sc. taeniopterus* spawns in the early morning, males holding day-time territories inshore could spawn near their offshore sleeping spots before returning in the morning. The fact that males at site M returned later in the morning than offshore migrators, yet had migrations that lasted as long, supports this view. Given the variability in mating systems known for *Sc. iserti*, it is possible that leks existed on the deep barrier reef where many site M males slept. *Sc. taeniopterus* may thus be less constrained than the other species to battling for space offshore.

The information presented here can neither confirm nor disprove the views of reef communities as being structured by classical niche specialization (Smith, 1978), or by stochastic processes (Sale, 1977, 1980). My observation that most juveniles recruit inshore, while reproduction takes place offshore, supports Sale's assertion that local recruitment is independent of the resident community. The fact that *Sp. viride* and *Sc. vetula* differed in distribution from the species I studied intensively, would seem to support the classical view. The coexistence of *Sp. aurofrenatum*, *Sc. taeniopterus*, and *Sc. iserti* is more difficult to explain on the basis of classical competition theories. The fact that each species' density varied in a different fashion from site to site points to subtle ecological differences between them. *Sc. taeniopterus* may replace *Sc. iserti* on deeper reefs (> 15 m) in Barbados, and was very uncommon in Panama. However, no species showed strongly contrasting associations with particular substrates or food categories. Each species allocated different amounts of time to its activities. Thus they are neither ecologically equivalent, nor narrowly specialized. Arguments that predation or particular resource utilization curves may allow competitively similar species to coexist (Roughgarden, 1974; Roughgarden and Feldman, 1975) remain to be tested. I suggest that coexistence of these species is possible because food levels are more than adequate to meet their needs, and space for reproduction is restricted only to other conspecifics.

Territoriality does appear to keep parrotfish numbers stable (e.g. Krebs, 1971). The numbers of Tph males in the three species studied here varied more over the year at site M, where territories were fewer and less exclusive, than at the offshore sites (average coefficient of variation inshore = 73.8, offshore C.V. = 38.1; Sokal and Rohlf, 1969). This difference did not appear for Iph fish which are less defensive of space than Tph males. The fact that Iph of some species increased in number between study periods indicates that their populations are less tightly constrained. Other factors such as recruitment and emigration also contribute to population stability.

In general, the role of female behaviour in population stability and social organization is poorly understood. The function of their aggression towards other females of similar sizes is not clear. It could reflect defence of food, but this seems unlikely considering how slightly food supply affected other aspects of parrotfish behaviour. Interactions between Iph and Tph appear to be important in harem maintenance, but for no simple reason. Males were not just herding females back inside their borders. A future study should concentrate on the behaviour of females in harem groups. Improved long-term tagging methods would allow better dissection of their social interactions. Additions and removals of Iph fish could test for both Iph territoriality and the effects of Iph density on Tph behaviour. Whether harem members recognize neighbours and extra-haremic individuals should also be tested (e.g.

Thresher, 1979b).

Size appears to affect both Iph dominance and Tph success. It is often assumed that large males are more successful than small ones (e.g. Warner, 1975b). My study reveals that there are also penalties for being too big. *Sp. aurofrenatum* on the barrier reef was restricted to the middle size ranges even though both larger and smaller males existed elsewhere. Perhaps aggressive displays become costly for large fish. The little time spent in aggression by the large males at site A support this view. Many fish species devote little time to aggressive activities, probably because of their high costs (Leum and Choat, 1980; Nursall, 1981; Jones, in press). The relatively large amounts of time that barrier reef males spent in aggression could have kept their growth rates low. Transfers of large and small males to experimentally emptied territories at the barrier reef might test the effects of size on successful territory defence.

Intruder males are a class of parrotfish that also require further study. The length of time spent in this state, the range of their movements, and the size of each species' intruder pool are unknown. Repeated removals of Tph residents might indicate the extent of the intruder population. It would also test whether first-come intruders are more capable of holding on to territories than later ones, i.e. whether a certain apprenticeship as an intruder is necessary before males can defend space. In my limited removal experiments, intruders who arrived at the end of the removal series were more likely to be evicted than were males in the first experiments. The cues that inform intruders when a space is available are also unknown, but the behavioural switch from sneaking through territories to open patrolling is very rapid. Perhaps intruders begin to display in an area if they have not been attacked after a certain lapse of time. This short-term flexibility applies to labroids undergoing sex change as well (Robertson, 1972, 1973).

Flexibility is a general mark of parrotfish behaviour. Iph *Scarus* can mass in schools, join loose feeding associations, or be territorial. Iph *Sp. aurofrenatum* can have both tightly site-attached and transient members. Some *Scarus* apparently judge their territories' suitability for night-time cover, and commute regularly to preferred sleeping spots (Dubin and Baker, 1981). Tph *Sp. aurofrenatum* can form alliances in areas where spawning is not a regular occurrence. All the species studied here can alter their grazing habits to match local availability. While some of these trends reflect life history stages, others are adaptive responses to the environment. Spawning site suitability, rather than shelter, competitors or food supply appears to be the major determinant of these species' social systems. The surprising result is their relative independence from the resources that are traditionally assumed to be crucial. The belief that food or shelter must limit numbers may result from the profusion of ecological studies that deal with animals living in seasonal environments, particularly birds with young to feed. As Sale (op. cit.) has argued, coral reefs may operate under a somewhat different set of constraints than other ecosystems. While a compromise view may eventually be reached, the controversies that precede it will extend our understanding of ecological principles as a whole, and their impact on social organization.

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Appendix 1. Correlation analysis of parrotfish spatial distribution patterns.

Appendix 1A. Site M: Spearman's correlations between number of parrotfish per quadrat and substrate variables including depth. Significance level is indicated by asterisks:*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. n = 100

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
VARIABLE:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
DEPTH:														
1978-9	0.14	0.39 ***	0.68 ***	0.41 ***	-0.60 ***	0.07	-0.26 **	0.40 **	0.54 ***	0.15	-0.24 **	-0.08	0.53 ***	0.66 ***
1976-7	0.32 ***	0.17 *	0.72 ***	0.56 ***	-0.34 ***	0.16	-0.14	0.16	0.51 ***	0.33 ***	-0.28 **	-0.09	0.59 ***	0.62 ***
%SAND:														
1978-9	-0.02	0.23 *	-0.03	0.14	-0.10	0.30 ***	-0.19 *	-0.09	-0.07	0.03	-0.08	-0.11	0.08	0.11
1976-7	0.14	-0.16	-0.09	0.13	-0.08	0.25 **	-0.10	-0.10	-0.07	-0.17 *	-0.20 *	-0.16	0.02	0.11
%RUBBLE:														
1978-9	0.40 ***	0.08	0.27 **	-0.05	0.01	-0.08	0.15	0.40 ***	0.32 ***	-0.33 ***	-0.05	0.21 *	0.24 **	0.16
1976-7	0.39 ***	-0.07	0.42 ***	-0.07	0.03	0.02	0.27 **	0.39 ***	0.35 ***	0.03	0.26 **	0.32 ***	0.11	0.08
%LARGE HEADS:														
1978-9	-0.09	0.20 *	0.09	0.12	0.00	0.12	-0.09	-0.11	-0.18 *	0.16	-0.06	-0.07	0.16	0.15
1976-7	0.02	0.01	-0.12	0.29 **	0.04	0.30 ***	-0.17 *	-0.18 *	-0.25 **	0.08	-0.20 *	-0.03	0.30 ***	0.32 ***
%SMALL HEADS:														
1978-9	-0.12	0.14	-0.22 *	-0.05	-0.04	-0.03	-0.31 ***	-0.34 ***	-0.26 **	0.00	-0.25 **	-0.00	-0.21 *	-0.12
1976-7	-0.12	0.13	-0.41 ***	-0.18 *	-0.17 *	-0.06	-0.28 **	-0.30 ***	-0.23 **	-0.30 ***	-0.10	-0.13	-0.14	-0.03
%STAGHORN:														
1978-9	-0.36 ***	-0.18 *	-0.38 ***	-0.09	0.41 ***	0.14	-0.07	-0.45 ***	-0.51 ***	0.13	-0.12	0.03	-0.07	-0.25 **
1976-7	-0.50 ***	-0.15	-0.46 ***	-0.19 *	0.31 ***	0.03	-0.22 *	-0.46 ***	-0.48 ***	0.20 *	-0.21 *	-0.08	-0.11	-0.25 **
%FINGER CORALS:														
1978-9	0.23 *	-0.06	0.26 **	0.17 *	-0.15	-0.19 *	0.29 **	0.33 ***	0.47 ***	-0.02	0.29 **	0.11	-0.06	-0.04
1976-7	0.15	0.08	0.39 ***	0.02	-0.12	-0.14	0.30 ***	0.33 ***	0.31 ***	-0.13	0.26 **	0.17 *	-0.14	-0.13
%DEAD CORAL:														
1978-9	-0.23 **	0.18 *	-0.03	0.17 *	-0.02	0.03	-0.30 ***	-0.19 *	-0.17 *	0.27 **	-0.19 *	-0.20 *	0.00	0.04
1976-7	-0.22 *	0.09	-0.27 **	0.21 *	-0.10	0.06	-0.41 ***	-0.40 ***	-0.26 **	0.05	-0.38 ***	-0.14	0.18 *	0.20 *

Appendix 1B. Site A: Spearman's correlations between number of parrotfish per quadrat and substrate variables. Significance level is indicated by asterisks: *: P < 0.05; **: P < 0.01; ***: P < 0.001. n = 50

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
VARIABLE:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
%SAND AND RUBBLE:	0.08	0.01	0.18	-0.25 *	-0.26 *	ND	0.08	0.29 *	-0.03	0.11	-0.18	0.03	ND	ND
%LARGE HEADS:	-0.12	0.05	-0.20	-0.03	-0.04	ND	-0.42 ***	-0.06	-0.20	-0.09	-0.04	0.05	ND	ND
%STAGHORN:	-0.03	-0.01	-0.06	0.16	0.32 *	ND	-0.06	-0.28 *	0.09	-0.12	0.19	0.02	ND	ND
%FINGER CORALS:	-0.10	0.05	-0.07	0.11	-0.04	ND	0.27 *	0.21	0.14	-0.01	-0.03	0.01	ND	ND
%DEAD CORAL:	-0.08	-0.01	-0.17	0.25 *	0.28 *	ND	-0.08	-0.29 *	0.04	-0.10	0.18	-0.03	ND	ND

Appendix 1C. Sites B and P: Spearman's correlations between number of parrotfish per quadrat and substrate variables. Significance level is indicated by asterisks.*: P < 0.05; **: P < 0.01; ***: P < 0.001. n = 50

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
VARIABLE:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
%SAND AND RUBBLE: Site B:														
1978-9	-0.17	-0.27 *	0.01	-0.02	-0.04	0.06	-0.41 ***	-0.17	0.36 **	0.17	-0.07	-0.04	-0.24 *	-0.20
1976-7	0.03	-0.01	0.14	-0.02	ND	ND	ND	0.30 *	0.44 ***	0.08	ND	-0.05	ND	ND
Site P:														
1978-9	0.22	0.03	-0.18	-0.07	-0.34 **	-0.20	0.06	0.35 **	0.33 **	-0.31 **	0.12	-0.20	-0.10	-0.18

Appendix 1D. Spearman's correlations between number of parrotfish per quadrat and number of damselfish. Significance level is indicated by asterisks:*: P < 0.05; **: P < 0.01; ***: P < 0.001. Damselfish number per quadrat (range) shown.

SPECIES:	*Sc. iserti* Iph	Tph	*Sc. taeniopterus* Iph	Tph	*Sc. vetula* Iph	Tph	*Scarus* juv.	*Sp. aurofrenatum* juv.	Iph	Tph	*Sp. viride* juv.	Iph-S	Iph-L	Tph
Site M:														
E. planifrons 13.8 (0-53)														
1978-9:	-0.27 **	-0.22 *	-0.47 ***	0.05	0.66 ***	0.16	0.04	-0.61 ***	-0.63 ***	0.22 *	0.00	0.14	-0.19 *	-0.42 ***
1976-7:	-0.46 ***	-0.07	-0.61 ***	-0.19 *	0.49 ***	-0.02	-0.13	-0.54 ***	-0.62 ***	0.09	-0.07	0.01	-0.19 *	-0.30 ***
E. partitus 23.7 (2-85)														
1978-9:	0.51 ***	0.21 *	0.58 ***	0.03	-0.08	-0.20 *	0.29 **	0.55 ***	0.67 ***	-0.03	0.16	0.29 ***	0.18 *	0.28 **
1976-7:	0.41 ***	0.08	0.64 ***	0.23 *	-0.05	-0.10	0.32 ***	0.42 ***	0.44 ***	0.12	0.29 **	0.38 ***	0.15	0.18 *
E. spp 1.0 (0-6)														
1978-9:	-0.04	0.19 *	-0.14	0.10	-0.19 *	0.01	-0.26 **	-0.21 *	-0.17 *	0.14	-0.08	-0.04	-0.21 *	-0.02
1976-7:	0.07	0.32 ***	-0.25 **	0.03	-0.27 **	-0.00	-0.31 ***	-0.15	0.01	-0.18 *	-0.04	-0.24 **	-0.05	0.09
Site A:														
E. planifrons 15.0 (2-27)														
1978-9	-0.16	-0.17	-0.20	0.08	0.11	ND	-0.44 ***	-0.26 *	-0.05	0.37 **	-0.01	0.11	ND	ND
E. partitus 22.9 (3-51)														
1978-9:	-0.10	-0.18	-0.09	0.11	0.21	ND	0.01	-0.13	-0.01	0.11	-0.04	0.08	ND	ND
Site B:														
E. planifrons 1.4 (0-8)														
1978-9:	-0.23	0.09	-0.38 *	0.20	0.13	-0.02	0.18	0.00	-0.48 ***	-0.10	0.10	-0.13	0.25 *	0.18
1976-7:	0.31 *	0.23	-0.16	0.07	ND	ND	ND	-0.02	-0.34 ***	-0.21	ND	0.06	ND	ND
E. partitus 25.9 (8-54)														
1978-9:	0.52 ***	0.25 *	0.04	-0.17	-0.06	-0.15	0.42 ***	0.13	-0.16	0.01	0.13	-0.05	-0.02	-0.10
1976-7:	0.26 *	0.26 *	-0.01	-0.15	ND	ND	ND	-0.11	-0.17	-0.22	ND	0.14	ND	ND
Site P:														
E. planifrons 0.8 (0-8)														
1978-9:	0.07	-0.20	0.03	-0.07	0.34 **	-0.03	-0.05	-0.32 *	-0.18	0.25 *	-0.21	0.22	0.03	0.05
E. partitus 22.5 (11-37)														
1978-9:	-0.12	0.14	0.01	0.07	0.29 *	0.10	0.00	0.03	-0.10	0.14	-0.05	-0.17	0.28 *	-0.04

Appendix 1E. Site M: 1978-9 Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: P < 0.05; **: P < 0.01; ***: P < 0.001. n = 100.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	1.00													
Tph	0.23 **	1.00												
Sc. taeniopterus														
Iph	0.55 ***	0.37 ***	1.00											
Tph	0.00	0.24 **	0.18 *	1.00										
Sc. vetula														
Iph	0.18 *	-0.18 *	-0.24 **	-0.05	1.00									
Tph	-0.13	0.07	-0.08	0.14	0.07	1.00								
Scarus juv.	0.39 ***	-0.17 *	0.07	-0.30 ***	0.42 ***	-0.17 *	1.00							
Sp. aurofrenatum														
juv.	0.41 ***	0.11	0.45 ***	-0.08	-0.25 **	-0.21 *	0.35 ***	1.00						
Iph	0.56 ***	0.23 *	0.62 ***	0.10	-0.32 ***	-0.14	0.14	0.62 ***	1.00					
Tph	-0.14	0.14	0.11	0.27 **	-0.06	0.06	-0.17 *	-0.22 *	-0.07	1.00				
Sp. viride														
juv.	0.28 **	-0.19 *	-0.02	-0.16	0.25 **	-0.37 ***	0.70 ***	0.33 ***	0.12	-0.08	1.00			
Iph-small	0.36 ***	0.18 *	0.12	-0.09	0.44 ***	0.00	0.30 ***	0.08	0.16	0.03	0.15	1.00		
Iph-large	0.01	0.27 **	0.43 ***	0.28 **	-0.15	0.28 **	-0.06	0.22 *	0.16 *	0.19 *	-0.25 **	0.12	1.00	
Tph	0.04	0.28 **	0.49 ***	0.30 ***	-0.50 ***	0.21 *	-0.32 ***	0.15	0.28 **	0.18 *	-0.35 ***	-0.07	0.54 ***	1.00

continued.......................

Appendix 1E continued. Site M: 1976-7. Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $n = 100$.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	1.00													
Tph	0.23 **	1.00												
Sc. taeniopterus														
Iph	0.53 ***	0.07	1.00											
Tph	0.13	0.20 *	0.32 ***	1.00										
Sc. vetula														
Iph	0.04	-0.15	-0.06	-0.32 ***	1.00									
Tph	0.09	-0.06	0.04	0.18 *	-0.04	1.00								
Scarus juv.	0.30 ***	-0.04	0.22 *	-0.13	0.28 **	-0.12	1.00							
Sp. aurofrenatum														
juv.	0.43 ***	0.02	0.40 ***	0.05	-0.05	-0.13	0.56 ***	1.00						
Iph	0.54 ***	0.17 *	0.65 ***	0.13	-0.12	-0.01	0.16	0.48 ***	1.00					
Tph	0.14	-0.06	0.25 **	0.27 **	0.03	0.13	-0.09	-0.11	0.20 *	1.00				
Sp. viride														
juv.	0.27 **	0.04	0.05	-0.25 **	0.26 **	-0.29 ***	0.71 ***	0.40 ***	0.07	-0.13	1.00			
Iph-small	0.38 ***	-0.08	0.41 ***	-0.06	0.49 ***	0.05	0.37 ***	0.19 *	0.20 *	0.06	0.38 ***	1.00		
Iph-large	0.18 *	-0.04	0.38 ***	0.52 **	-0.18 *	0.41 ***	-0.17 *	-0.05	0.21 *	0.44 ***	-0.18 *	0.19 *	1.00	
Tph	0.19 *	0.02	0.34 **	0.53 ***	-0.33 ***	0.28 **	-0.16	-0.03	0.17 *	0.36 ***	-0.26 **	0.04	0.66 ***	1.00

continued........................

Appendix 1E continued. Site A: 1979 Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: P < 0.05; **: P < 0.01; ***: P < 0.001. n = 50.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	1.00													
Tph	0.26 *	1.00												
Sc. taeniopterus														
Iph	0.42 ***	0.01	1.00											
Tph	0.36 **	0.27 *	-0.10	1.00										
Sc. vetula														
Iph	0.12	-0.19	0.14	-0.04	1.00									
Tph	ND	ND	ND	ND	ND	ND								
Scarus juv.	0.27 *	0.19	0.42 ***	-0.10	0.12	ND	1.00							
Sp. aurofrenatum														
juv.	0.33 **	-0.01	0.37 **	-0.14	0.02	ND	0.40 **	1.00						
Iph	0.07	0.27 *	0.12	-0.10	0.18	ND	0.13	0.17	1.00					
Tph	-0.14	-0.14	-0.25 *	0.20	0.01	ND	-0.35 **	-0.07	0.20	1.00				
Sp. viride														
juv.	0.05	-0.19	0.07	-0.20	0.15	ND	-0.08	0.18	0.03	0.09	1.00			
Iph-small	-0.07	-0.03	0.09	-0.12	-0.05	ND	0.12	0.20	-0.01	-0.05	-0.10	1.00		
Iph-large	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	
Tph	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

continued........................

Appendix 1E continued. Site B: 1978-9. Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $n = 50$.

SPECIES:	*Sc. iserti* Iph	*Sc. iserti* Tph	*Sc. taeniopterus* Iph	*Sc. taeniopterus* Tph	*Sc. vetula* Iph	*Sc. vetula* Tph	*Scarus* juv.	*Sp. aurofrenatum* juv.	*Sp. aurofrenatum* Iph	*Sp. aurofrenatum* Tph	*Sp. viride* juv.	*Sp. viride* Iph-S	*Sp. viride* Iph-L	*Sp. viride* Tph
Sc. iserti														
Iph	1.00													
Tph	0.33 **	1.00												
Sc. taeniopterus														
Iph	0.31 *	-0.04	1.00											
Tph	-0.13	0.07	-0.21	1.00										
Sc. vetula														
Iph	0.07	-0.11	-0.09	0.09	1.00									
Tph	ND	ND	ND	ND	ND	ND								
Scarus juv.	0.46 ***	0.41 **	0.17	0.05	0.07	ND	1.00							
Sp. aurofrenatum														
juv.	0.51 ***	-0.34 **	0.21	0.18	0.11	ND	0.58 ***	1.00						
Iph	0.12	0.03	0.21	-0.01	-0.11	ND	-0.06	0.20	1.00					
Tph	0.10	-0.13	0.10	0.03	0.21	ND	0.04	0.02	0.12	1.00				
Sp. viride														
juv.	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND			
Iph-small	0.09	-0.06	0.19	0.07	-0.04	ND	0.08	0.11	0.21	-0.33 **	ND	1.00		
Iph-large	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	
Tph	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

continued........................

Appendix 1E continued. Site B: 1976-7. Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $n = 50$.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	1.00													
Tph	0.28*	1.00												
Sc. taeniopterus														
Iph	0.19	0.19	1.00											
Tph	-0.14	0.01	-0.15	1.00										
Sc. vetula														
Iph	-0.15	-0.03	-0.17	0.14	1.00									
Tph	ND	ND	ND	ND	ND	ND								
Scarus juv.	ND	ND	ND	ND	ND	ND	ND							
Sp. aurofrenatum														
juv.	0.21	0.12	0.09	-0.11	0.02	ND	ND	1.00						
Iph	0.09	-0.04	0.22	0.08	0.24*	ND	ND	0.15	1.00					
Tph	-0.31*	-0.14	0.03	-0.09	0.16	ND	ND	-0.05	0.02	1.00				
Sp. viride														
juv.	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND			
Iph-small	0.24*	0.25*	0.17	0.01	-0.05	ND	ND	-0.06	-0.02	-0.28*	ND	1.00		
Iph-large	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	
Tph	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

continued.......................

Appendix 1E continued. Site P: 1978-9. Spearman's correlation matrix between number of parrotfish per quadrat. Significance level is indicated by asterisks: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $n = 50$.

	Sc. iserti		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
SPECIES:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Sc. iserti														
Iph	1.00													
Tph	0.21	1.00												
Sc. taeniopterus														
Iph	0.14	0.02	1.00											
Tph	-0.30 *	0.27 *	-0.07	1.00										
Sc. vetula														
Iph	-0.11	-0.03	0.11	0.04	1.00									
Tph	0.13	0.34 **	0.21	-0.05	0.01	1.00								
Scarus juv.	-0.04	-0.02	0.15	-0.03	0.04	-0.09	1.00							
Sp. aurofrenatum														
juv.	0.18	-0.19	0.01	-0.18	-0.22	0.00	0.08	1.00						
Iph	0.48 ***	0.02	-0.04	-0.26 *	-0.24 *	0.04	-0.18	0.18	1.00					
Tph	0.22	0.08	0.13	-0.06	0.33 **	0.02	0.06	-0.34 **	-0.04	1.00				
Sp. viride														
juv.	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND			
Iph-small	0.03	-0.17	0.01	0.14	-0.03	-0.01	-0.11	-0.23	0.00	-0.11	ND	1.00		
Iph-large	0.04	-0.04	0.44 ***	-0.10	-0.07	0.14	0.25 *	0.05	-0.01	-0.17	ND	0.15	ND	
Tph	0.19	0.18	0.35 **	0.04	0.05	0.20	-0.09	-0.31 **	0.13	0.14	ND	0.30 *	0.06	ND

C

Appendix 1F. Juvenile scarids: percent of time seen with at least one other parrotfish during grid surveys, and percent of total sightings with each species. Values for sites M and B are totals for 1976-7 plus 1978-9. Total sightings in parentheses.

	TOTAL	SEEN WITH: *Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
	PERCENT:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
juv. *Scarus*															
Site M (5102)	96.1	6.9	0.0	4.1	0.0	4.5	0.0	94.1	12.5	0.7	0.0	24.7	2.3	0.0	0.0
Site A (65)	86.2	9.2	0.0	20.0	0.0	4.6	0.0	75.4	32.3	3.1	0.0	1.5	0.0	0.0	0.0
Site B (47)	52.9	0.0	0.0	8.5	0.0	0.0	0.0	27.7	40.4	0.0	0.0	2.1	0.0	0.0	0.0
Site P (123)	63.4	4.9	0.8	1.6	0.0	0.0	0.0	51.2	17.9	0.8	0.0	1.6	0.8	0.0	0.0
juv. *Sp. aurofrenatum*															
Site M (467)	45.9	6.6	0.0	5.0	0.0	2.4	0.0	27.6	20.4	2.2	0.0	9.2	0.7	0.0	0.0
Site A (48)	56.3	6.3	0.0	20.8	0.0	0.0	0.0	35.4	25.0	4.2	0.0	2.1	0.0	0.0	0.0
Site B (192)	37.6	4.2	0.5	6.8	0.0	0.0	0.0	9.9	18.8	0.5	0.0	0.5	0.0	0.0	0.0
Site P (190)	32.1	4.2	0.5	1.1	0.0	0.0	0.0	9.5	21.1	1.6	0.0	0.0	0.0	0.0	0.0
juv. *Sp. viride*															
Site M (768)	51.5	5.2	0.0	0.9	0.0	2.1	0.0	31.9	5.6	0.7	0.0	26.6	1.6	0.0	0.0
Site A (14)	7.1	0.0	0.0	7.1	0.0	0.0	0.0	7.1	7.1	0.0	0.0	0.0	0.0	0.0	0.0
Site B (4)	25.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Site P (7)	28.6	14.3	0.0	0.0	0.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

continued......................

Appendix 1F continued: Iph scarids.

	TOTAL PERCENT:	SEEN WITH: *Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
		Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Iph *Sc. iserti*															
Site M (9600)	81.5	71.2	15.6	12.2	0.1	13.7	0.1	2.6	1.0	8.4	0.04	1.1	7.1	0.1	0.01
Site A (54)	55.6	48.1	0.0	35.2	0.0	0.0	0.0	11.1	13.0	3.7	0.0	0.0	0.0	0.0	0.0
Site B (4823)	68.4	58.7	5.0	15.8	0.02	0.2	0.0	0.0	0.2	6.[illegible]	0.2	0.0	0.4	0.0	0.0
Site P (4313)	71.6	69.3	9.8	4.8	0.02	0.2	0.0	0.5	0.7	8.1	0.02	0.1	0.5	0.0	0.0
Iph *Sc. taeniopterus*															
Site M (2525)	65.4	38.3	0.8	50.0	0.8	9.1	0.2	2.3	2.6	7.7	0.2	1.7	4.6	0.2	0.2
Site A (168)	62.5	8.9	1.2	56.0	0.0	0.0	0.0	7.1	11.9	5.4	0.0	1.2	1.2	0.0	0.0
Site B (2416)	70.4	33.3	3.7	58.7	0.9	0.1	0.0	0.1	0.9	6.8	0.2	0.0	0.9	0.0	0.0
Site P (667)	28.2	12.4	3.4	20.4	0.4	0.0	0.0	0.4	0.9	2.5	0.0	0.0	0.1	0.0	0.0
Iph *Sc. vetula*															
Site M (1789)	48.0	25.8	0.6	8.7	0.2	32.5	0.8	3.1	0.8	3.7	0.1	1.3	6.3	0.4	0.1
Site A (14)	21.4	0.0	0.0	0.0	0.0	14.0	0.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site B (64)	43.1	9.4	0.0	3.1	0.0	26.6	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0
Site P (79)	7.6	2.5	2.5	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0
Iph *Sp. aurofrenatum*															
Site M (1138)	35.7	20.8	0.4	9.6	0.3	4.2	0.1	0.8	0.9	10.1	1.1	0.5	5.4	0.1	0.0
Site A (64)	14.1	1.6	0.0	10.9	0.0	0.0	0.0	1.6	3.2	3.2	0.0	0.0	1.6	0.0	0.0
Site B (1296)	21.4	10.3	1.0	5.3	0.0	0.1	0.0	0.0	0.1	9.0	1.7	0.0	1.2	0.0	0.0
Site P (1056)	20.0	11.4	0.9	1.1	0.0	0.0	0.0	0.1	0.3	7.4	1.8	0.0	0.7	0.1	0.1

continued......................

Appendix.1F continued: Iph and Tph scarids.

	TOTAL	SEEN WITH: Sc. *iserti*		Sc. *taeniopterus*		Sc. *vetula*		*Scarus*	Sp. *aurofrenatum*			Sp. *viride*			
	PERCENT:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Iph Sp. *viride*: small															
Site M (1953)	24.9	10.1	0.2	4.2	0.1	4.4	0.4	0.9	0.2	3.2	0.2	0.6	11.3	0.6	0.0
Site A (41)	17.1	0.0	0.0	4.8	2.4	0.0	0.0	0.0	0.0	2.4	2.4	0.0	7.3	0.0	0.0
Site B (153)	11.5	4.6	0.0	3.9	0.7	0.0	0.0	0.0	0.0	3.3	0.7	0.0	5.9	0.0	0.0
Site P (291)	6.9	3.4	0.0	0.3	0.0	0.0	0.0	0.3	0.0	2.1	0.3	0.0	2.4	0.0	0.3
Iph Sp. *viride* :large															
Site M (499)	75.9	1.4	0.0	9.8	1.8	3.2	6.6	0.0	0.0	0.2	3.0	0.0	4.4	66.7	35.1
Site A (0)															
Site B (8)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site P (75)	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	2.6	1.3
Tph scarids:															
Tph Sc. *iserti*															
Site M (252)	32.9	21.8	4.0	4.4	0.0	2.4	0.0	1.2	0.0	2.0	0.0	0.0	1.2	0.0	0.0
Site A (15)	13.3	0.0	0.0	13.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site B (984)	23.0	15.4	1.2	4.4	0.0	0.0	0.0	0.0	0.1	1.6	0.1	0.0	0.0	0.0	0.0
Site P (679)	22.5	19.1	2.7	2.2	0.0	0.3	0.0	0.0	0.1	1.2	0.0	0.0	0.0	0.0	0.0
Tph Sc. *taeniopterus*															
Site M (235)	11.2	2.6	0.0	6.4	3.8	1.7	0.9	0.0	0.0	0.4	0.0	0.0	0.4	0.8	0.8
Site A (25)	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0
Site B (260)	8.1	0.4	0.0	8.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Site P (123)	3.3	0.8	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0

continued.......................

Appendix 1F continued: Tph scarids.

	TOTAL	SEEN WITH: *Sc. iserti*		*Sc. taeniopterus*		*Sc. vetula*		*Scarus*	*Sp. aurofrenatum*			*Sp. viride*			
	PERCENT:	Iph	Tph	Iph	Tph	Iph	Tph	juv.	juv.	Iph	Tph	juv.	Iph-S	Iph-L	Tph
Tph *Sc. vetula*															
Site M (250)	17.7	1.6	0.0	1.2	0.8	5.6	3.2	0.0	0.0	0.4	0.4	0.0	2.4	5.6	2.0
Site A (2)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site B (7)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site P (32)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tph *Sp. aurofrenatum*															
Site M (241)	8.8	0.8	0.0	1.2	0.4	0.8	0.4	0.0	0.0	2.5	2.9	0.0	0.8	0.8	0.8
Site A (22)	13.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.0	0.0	4.5	0.0	0.0
Site B (458)	8.7	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	4.4	4.1	0.0	0.2	0.0	0.2
Site P (377)	15.7	0.3	0.0	0.3	0.3	0.0	0.0	0.0	0.0	4.8	10.1	0.0	0.3	0.0	0.0
Tph *Sp. viride*															
Site M (159)	60.3	0.6	0.0	3.8	3.1	2.5	6.3	0.0	0.0	0.0	4.4	0.0	10.7	45.3	34.6
Site A (2)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site B (2)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Site P (47)	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	2.1	2.1	0.0

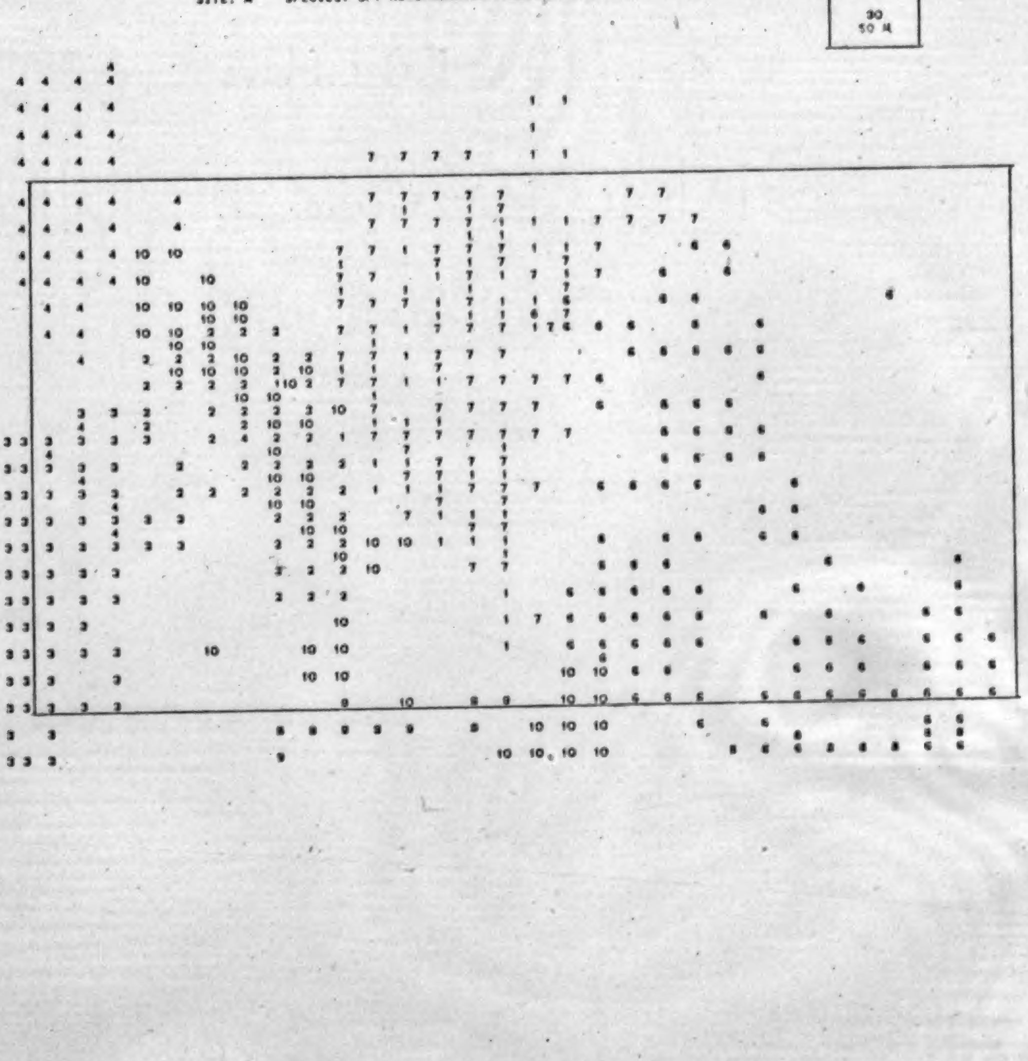
Appendix 2. Computer maps of parrotfish territories and home ranges in 1978-9.

Offshore (west) end points to the left. Unidentified individuals are denoted by letters. Individuals that were identified are denoted by numbers. The position of the individual's number or letter within the study area indicates a 6 m^2 sub-quadrat which the individual entered at least once during activity budget sampling (see Chapter 2). Overlaps where two or more fish used the same quadrat are shown by writing the individuals' numbers or letters above one another or side by side.

SITE: M SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 18/ 7/78 TO 28/ 7/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	19/ 7/78	***	186
	19/ 7/78	***	256
2	18/ 7/78	***	73
	18/ 7/78	11.5	208
3	22/ 7/78	***	253
	21/ 7/78	***	247
	24/ 7/78	***	316
4	21/ 7/78	***	182
	21/ 7/78	***	76
6	18/ 7/78	***	245
	18/ 7/78	12.0	126
	28/ 7/78	***	370
7	21/ 7/78	***	217
	22/ 7/78	***	338
8	28/ 7/78	4.5	***
9	28/ 7/78	7.0	***
10	22/ 7/78	***	144
	24/ 7/78	***	114

SITE: M SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 18/ 7/78 TO 28/ 7/78



SITE: M   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 12/ 1/79 TO 15/ 1/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
17	15/ 1/79	10.5	100
	15/ 1/79	17.5	170
18	12/ 1/79	18.0	125
	15/ 1/79	18.5	276
19	12/ 1/79	11.5	68
	10/ 1/79	9.0	118
21	10/ 1/79	11.0	167
	10/ 1/79	15.0	134
23	10/ 1/79	14.0	148
	10/ 1/79	14.0	131
25	12/ 1/79	15.0	34
	11/ 1/79	15.0	76
26	12/ 1/79	17.5	181
	10/ 1/79	15.5	409
28	11/ 1/79	16.0	66
	15/ 1/79	15.5	83
29	15/ 1/79	15.0	237
	15/ 1/79	15.0	167

```
                         SITE: M    SPECIES: SP. AUROFRENATUM PHASE: TPH  DATES: 12/ 1/79 TO 15/ 1/79
                                                                                                            30
                                                                                                          SQ M
                  18  18  18  18  18  18  18  18  18                                      29  29  29  29  29  29  29  29  29
                  18              18  18  18  18  18      28                              29  29  29  29  29  29  29  29
                  18  18  18  18  18  18  18  18  18      28  28                          29  29  29  29  29  29  29  29  29
                  18  18  18  18  18  18  18  18  18      28  28  28                      29  29  29  29  29  29  29  29  29
                  18  18  18  18  18  18  18  18  18      28      28                      29  29  29  29  29  29      29  21
          17  17  17  18          18  18      18  18  28  28  25  26                      29  29  29  29  29  29          21
                                                                      28
  17  17  17  17  17  17  18      18      18  18  18  28  25  26  28  25  25              29  29  29  29  29  29
                      17                          18
  17  17  17  17  17  18  18  18  18      18  18  28  28  28  28  28  25  25              29  29  29  29              21
                      17                          18
  17  17  17  17  17  18  18  18  18          18  28  28  28  28  28  25  25              29  29  29      29          21
                                                                  28  25  25
  17  17  17  17  17  17      18      18              28  28      25  192819  25  25      29  29  29  29
                                                                      25  25
  17  17  17  17  17  17  17          18              28          25  192819  25  25          29  29  29              21
1717  17  17  17  17  17  17      18  18                      26      19  19  25  25
                                                                          25
1717  17  17  17  17  17  17      18                      26  26      25  19  25  25                                  21
                                                                      25  25
      17  17  17  17  17          18  18                  26  26  28  19  19  25  25                          21  21
                                                                      25  25                              21
          17  17  17  17          18  18  26  26  26  26      26  26  19  19      25  25                  23  21
                                                                      26                                  21
                  17  17          18      26      26      26  26  26  192519      25  25                  23  23
                                                                      26  26
                  17  17              18  26                      26  26  19251925        25                  23  21  23
                                                                  26  26  26          21          23      21
                                  18  18  26  26      26  26  26  19  19  19          25  23      21      23
                                                                  26  26  26                      23  23  23
                                      18  26  26      26  26  26  19  19  19          21      23  21  21  21  23                  23
                                                                  26  25  19              21  23  23  23  21
                                          26  26          26  26  19  19  26      21  21  23  21  21  21  23  23                  23
                                                                      19  19              21  23  23      21
                                              26          26  26  19  26  26      21  21  23  21  21  23  23  21                  23
                                                                      19  19              23  23  21  21      23
                                              26      26  26  26  19  26  26  21  21  21  21  21  23  23  21  21                  23
                                                                  19  19  19          23  23  21  21  21  21  23
                                                  26  26  26      26  26  26  21  21  21  21  23  23  23  23  21                  23
                                                                  19  19                  23  23  21  21  21
                                                  26  26  26  26  26  26  19      21  21  21  21  23  23  23  21              23  23
                                                                  19  19                      23  23  21  23
                                                  26  26  26  26  26  26  19  21  21  21  21  21  21  23  21  23  23  23  23  23  23
                                                                                                          21
                                                          26  26  19  19              21  21  21  21  21  23  23  23  23  23
                                                                  19                      21  21  21  21          23  23  23
```

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SITE: M    SPECIES: SP. AUROFRENATUM PHASE: IPH  DATES: 30/ 1/79 TO  1/ 3/79

INDIVIDUAL      DATE       MINUTES WATCHED     AREA ENCLOSED (SQ M )

     1        12/ 2/79          10.0                 41
              31/ 1/79          12.0                120
              30/ 1/79          10.0                 38

     2        13/ 2/79          15.0                 60
              31/ 1/79          10.0                 67
              30/ 1/79          15.0                104

     3        12/ 2/79          10.0                 98
              30/ 1/79          11.0                 66

     4        13/ 2/79          15.0                 54
              12/ 2/79          11.5                 72

     5        13/ 2/79          11.0                 31
              12/ 2/79          11.5                 57

     6        15/ 2/79          15.0                 96
              15/ 2/79          16.0                110

     7        15/ 3/79          16.0                 88
              14/ 2/79          16.0                119

     8        14/ 2/79          11.5                 80
               1/ 3/79          15.5                101

     9        16/ 2/79          10.5                 58

     A        13/ 2/79           4.0                 45

     B        12/ 2/79           6.0                 47
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SITE: M    SPECIES: SP. AUROFRENATUM PHASE: IPH  DATES: 30/ 1/79 TO  1/ 3/79
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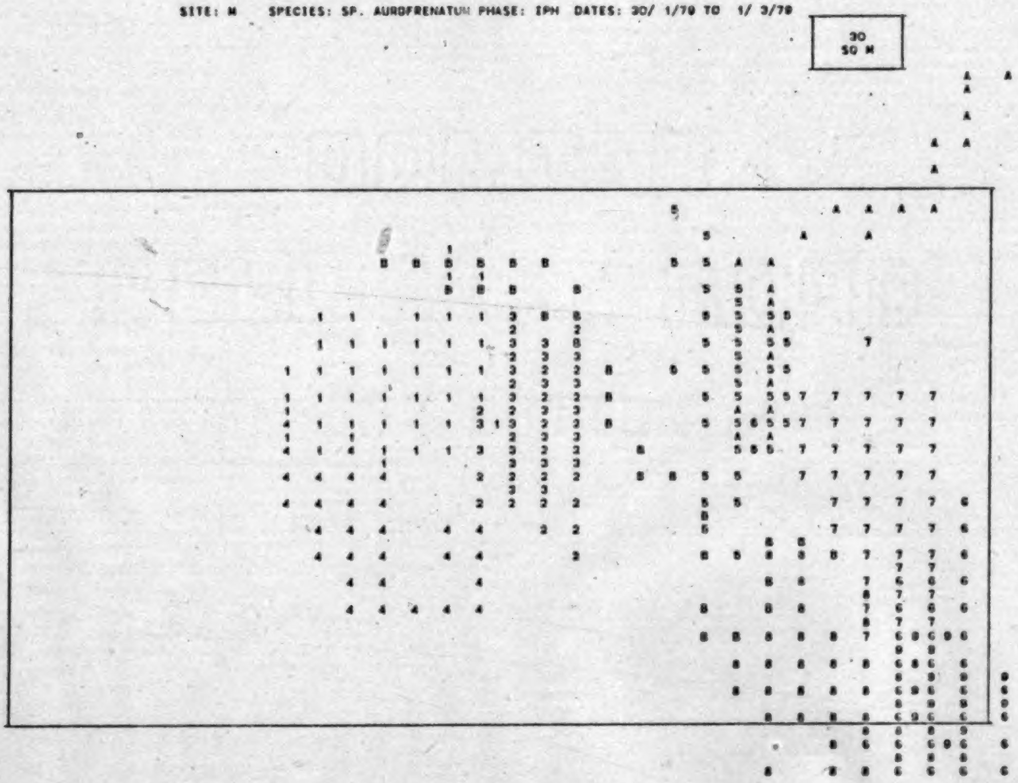
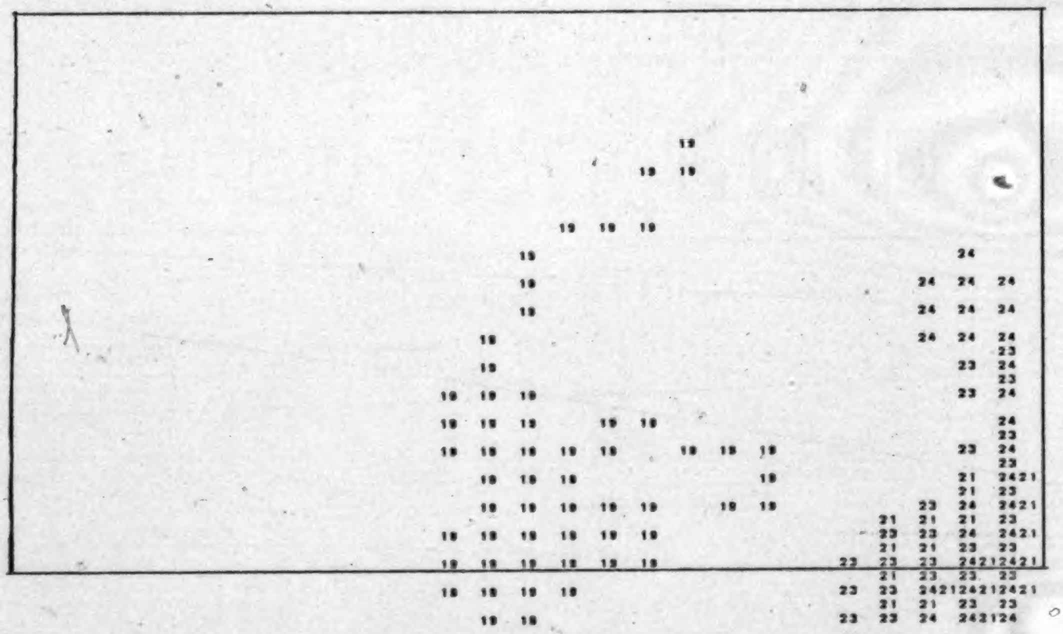


SITE: M SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 14/11/78 TO 17/12/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
19	17/12/78	15.0	73
	14/11/78	18.0	149
21	17/12/78	11.5	84
23	17/12/78	13.5	181
24	17/12/78	17.0	175

SITE: M SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 14/11/78 TO 17/12/78

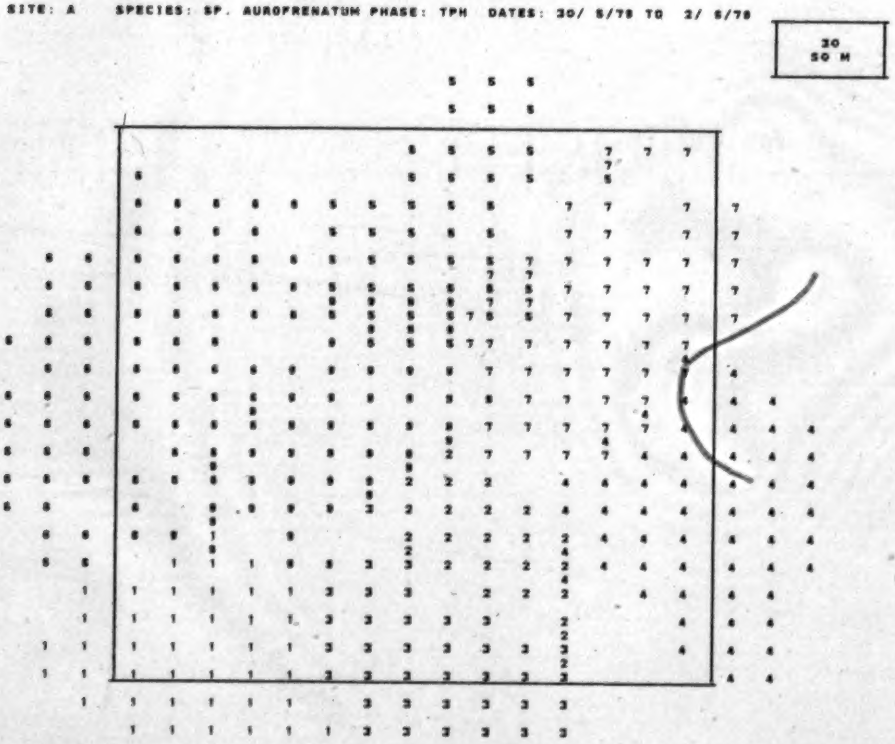
30
SQ M



SITE: A SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 30/ 5/78 TO 2/ 6/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	1/ 6/78	20.0	145
	30/ 5/78	20.0	185
2	30/ 5/78	20.0	80
	30/ 5/78	20.0	50
3	2/ 6/78	22.0	110
	1/ 6/78	20.0	145
4	31/ 5/78	20.0	155
	1/ 6/78	20.0	145
5	31/ 5/78	20.0	170
	30/ 5/78	20.0	75
6	1/ 6/78	20.0	280
	30/ 5/78	20.0	195
7	2/ 6/78	21.0	105
	31/ 5/78	21.0	210
8	31/ 5/78	21.0	115
	1/ 6/78	20.0	120

SITE: A SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 30/ 5/78 TO 2/ 6/78

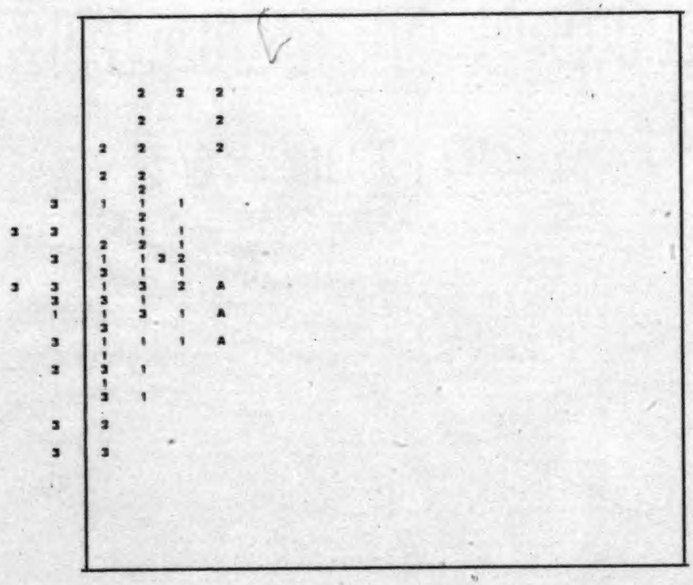


SITE: A SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 30/ 5/79 TO 22/ 6/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	22/ 6/79 30/ 5/79	11.0 15.0	50 60
2	22/ 6/79	14.5	22
3	22/ 6/79	12.0	55
A	22/ 6/79	10.0	10

SITE: A SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 30/ 5/79 TO 22/ 6/79

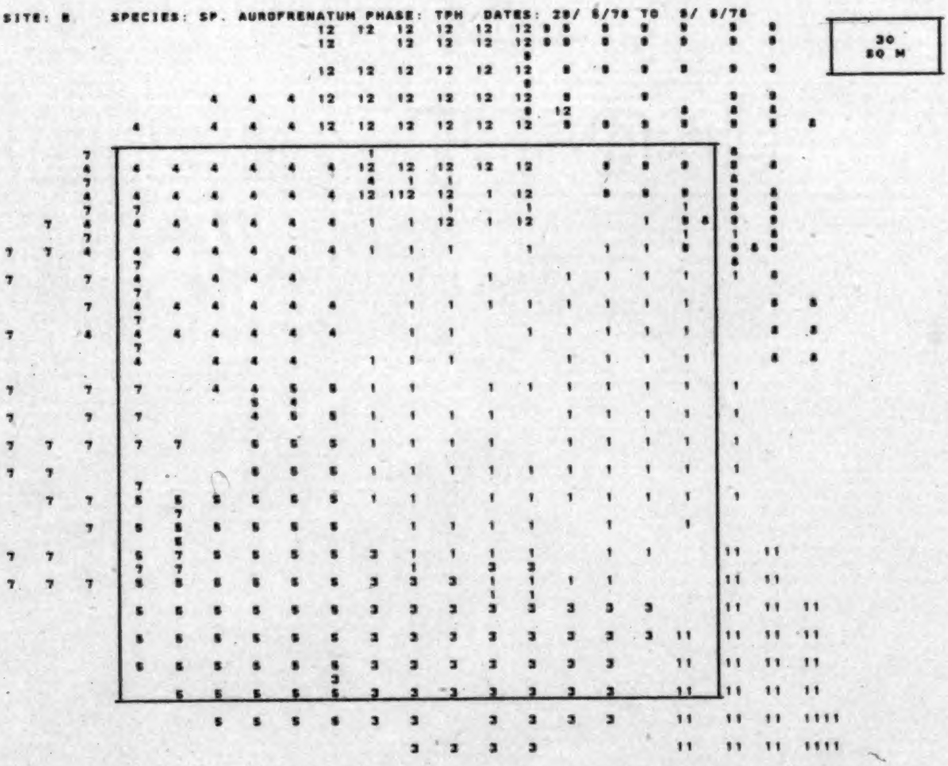
30
SQ M



SITE: B SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 29/ 5/78 TO 9/ 6/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (30 M)
1	29/ 5/78	12.0	617
	30/ 5/78	10.5	540
	2/ 6/78	12.0	583
3	29/ 5/78	7.0	218
	30/ 5/78	14.0	230
	2/ 6/78	9.0	224
4	29/ 5/78	10.0	221
	30/ 5/78	9.5	201
	2/ 6/78	11.0	192
5	29/ 5/78	7.0	137
	30/ 5/78	12.0	157
	2/ 6/78	10.5	186
7	30/ 5/78	10.0	280
8	30/ 5/78	9.5	***
9	8/ 6/78	10.5	***
	8/ 6/78	10.5	***
11	8/ 6/78	10.5	284
12	9/ 6/78	13.5	***
	9/ 6/78	13.5	***

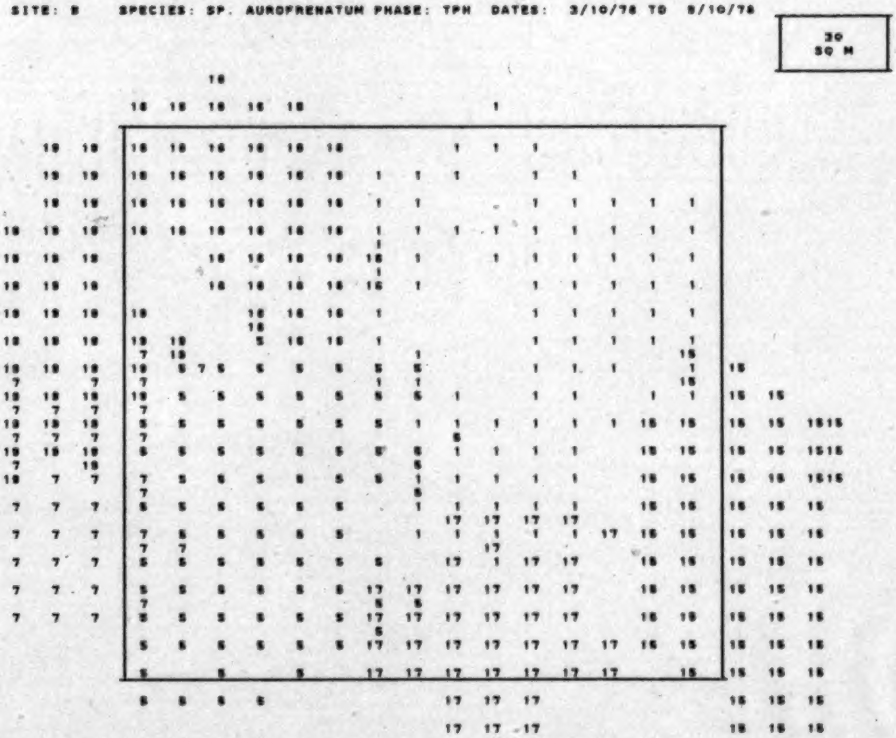
SITE: B. SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 29/ 5/78 TO 9/ 6/78



SITE: B SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 3/10/78 TO 5/10/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	3/10/78	14.0	515
	5/10/78	13.0	572
5	3/10/78	15.0	471
	4/10/78	10.0	205
7	4/10/78	15.0	131
	5/10/78	10.0	107
15	3/10/78	6.5	200
	5/10/78	13.5	372
16	3/10/78	14.0	214
	5/10/78	11.5	180
17	3/10/78	15.0	278
	5/10/78	10.0	220
19	4/10/78	11.5	185
	5/10/78	10.0	140

SITE: B SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 3/10/78 TO 5/10/78



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      19  19    16  16  16  16  16  16   1   1           1   1   1   1   1
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  19  19  19    19   5 7 5   5   5   5   5   5           1   1   1       1    15
   7       7     7                       1   1                           15
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                 7                           5
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                                                  17  17  17  17
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                 7   7                                17
   7   7   7     5   5   5   5   5   5   5      17   1  17  17      15  15    15  15  15
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                 7                       5   5
   7   7   7     5   5   5   5   5   5  17  17  17  17  17  17      15  15    15  15  15
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                 5       5       5      17  17  17  17  17  17  17      15    15  15  15
                 5   5   5   5                  17  17  17                    15  15  15
                                                17  17  17                    15  15  15
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SITE: B    SPECIES: SP. AUROFRENATUM PHASE: TPH  DATES:  6/12/78 TO  6/12/78
INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )
     1        6/12/78            22.5                371
     5        6/12/78            20.0                323
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SITE: B    SPECIES: SP. AUROFRENATUM PHASE: TPH  DATES:  5/12/78 TO  6/12/78
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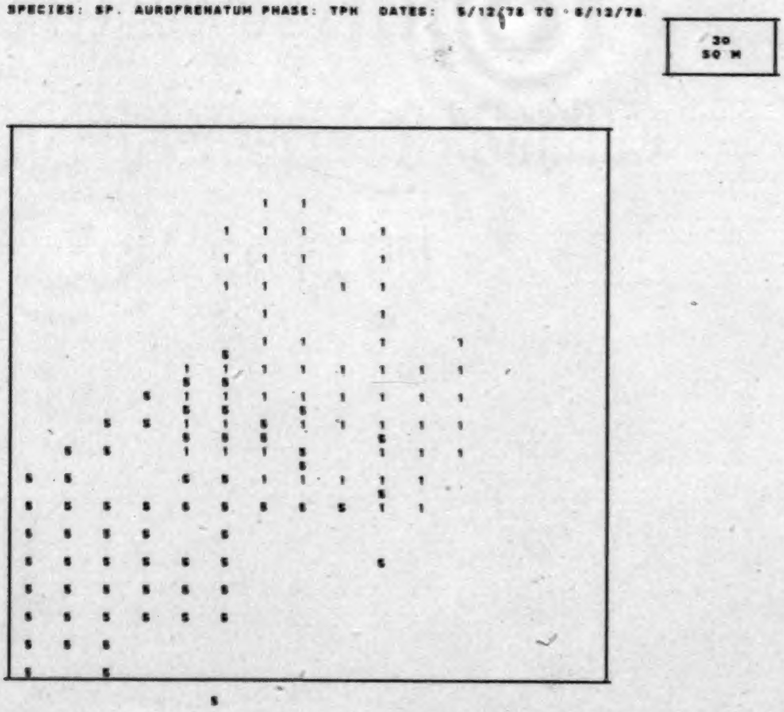

SITE: B   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 3/ 5/79 TO 10/ 5/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
5	4/ 5/79	18.0	330
	3/ 5/79	21.0	348
15	8/ 5/79	15.0	149
	4/ 5/79	15.0	110
19	8/ 5/79	15.0	170
	3/ 5/79	14.0	155
20	6/ 5/79	16.0	239
	4/ 5/79	15.0	307
27	9/ 5/79	18.0	284
	3/ 5/79	16.0	263
28	6/ 5/79	14.0	194
	4/ 5/79	15.0	144
31	9/ 5/79	15.0	258
	3/ 5/79	16.0	259
39	9/ 5/79	16.0	202
	10/ 5/79	18.0	138

SITE: B   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 3/ 5/79 TO 10/ 5/79

30
SQ M

```
            28
            28  28  28  28  28  28              20  20          20  20      20
                                                28
        19      28  28  28  28  28  28  28  28  20  28          20  20  20  20  20
                                                20  20
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                                                    20  28
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                    19                              28
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                                                20      20
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                                                20
    19  19  19  19  19      28  28  39  39  39  39  39  20  20  20  20
                                                        20
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                                                            31
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                                         5              31
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                                         5          27  31
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                                            27
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                                        27              31  27  31
             5   5   5   5   5   5   5   5  27  27  27  27  31  15  31  31  31  31
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                     5       5              27  27  27  27      15  15  15  15
                                                                    31  31
                                        27  27  27  27          15  15  15  31
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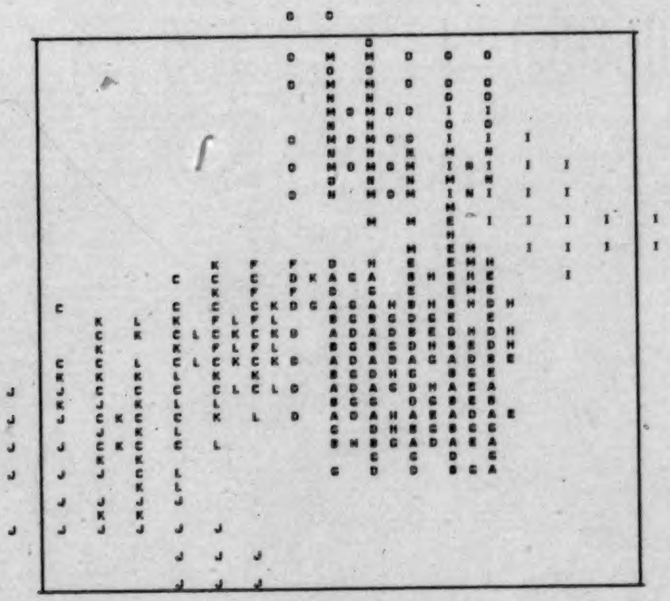
SITE: B SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 4/12/78 TO 5/12/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
A	5/12/78	10.0	104
B	5/12/78	11.0	124
C	5/12/78	14.5	107
D	5/12/78	15.5	57
E	5/12/78	8.0	82
F	5/12/78	2.0	28
G	5/12/78	5.5	95
H	5/12/78	11.0	150
I	5/12/78	10.0	93
J	4/12/78	10.0	88
K	4/12/78	13.5	94
L	4/12/78	10.0	85
M	4/12/78	9.5	82
N	4/12/78	5.5	78
O	5/12/78	8.5	158

SITE: B SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 4/12/78 TO 5/12/78

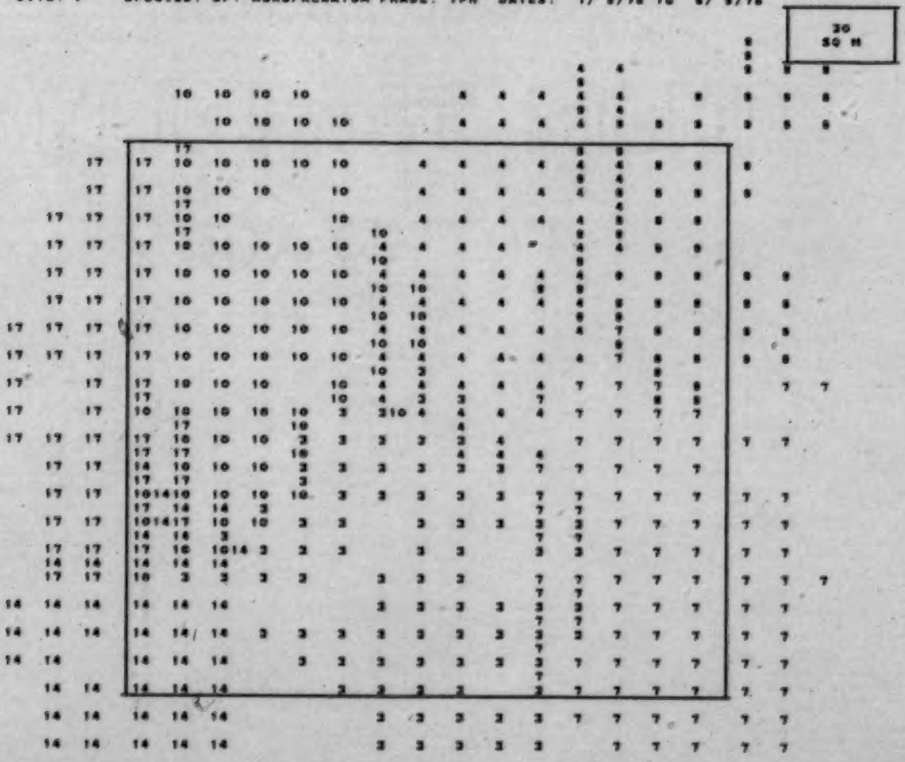
20
SQ M



SITE: P   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 1/ 8/78 TO 6/ 8/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
3	2/ 8/78	8.0	95
	3/ 8/78	14.5	280
	6/ 8/78	10.5	110
4	1/ 8/78	12.0	130
	3/ 8/78	22.0	195
	6/ 8/78	13.0	190
7	4/ 8/78	12.0	205
	5/ 8/78	19.0	225
	6/ 8/78	12.0	280
8	3/ 8/78	10.5	123
	2/ 8/78	11.0	105
	6/ 8/78	8.5	95
10	1/ 8/78	12.5	63
	3/ 8/78	13.0	160
	5/ 8/78	12.0	280
14	5/ 8/78	12.0	108
	6/ 8/78	13.5	190
17	4/ 8/78	14.5	103
	6/ 8/78	13.5	175

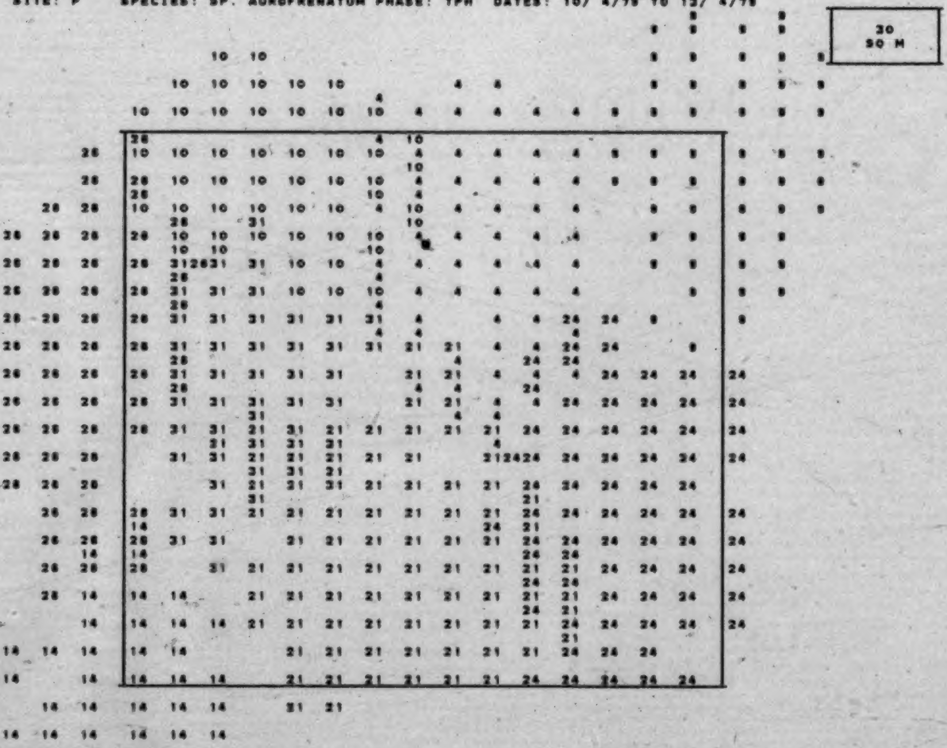
SITE: P   SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 1/ 8/78 TO 6/ 8/78



SITE: P SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 10/ 4/79 TO 13/ 4/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
4	13/ 4/79	15.0	210
	11/ 4/79	20.0	170
5	11/ 4/79	15.0	205
	11/ 4/79	20.0	150
10	10/ 4/79	15.5	135
	12/ 4/79	21.0	185
14	11/ 4/79	15.5	170
	13/ 4/79	15.0	142
21	10/ 4/79	20.0	250
	12/ 4/79	5.0	205
24	12/ 4/79	15.0	245
	11/ 4/79	20.0	230
25	11/ 4/79	15.0	155
	13/ 4/79	15.0	150
31	10/ 4/79	15.0	145
	12/ 4/79	20.0	135

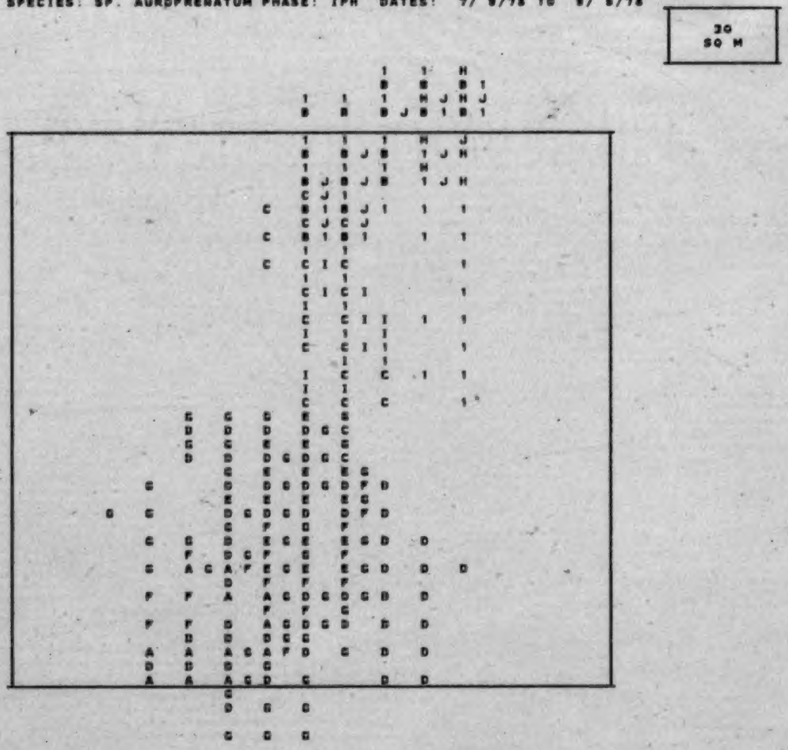
SITE: P SPECIES: SP. AUROFRENATUM PHASE: TPH DATES: 10/ 4/79 TO 13/ 4/79



SITE: P SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 7/ 8/78 TO 8/ 3/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	7/ 8/78 7/ 8/78	10.5 5.0	135 60
A	7/ 8/78	7.0	35
B	7/ 8/78	5.0	55
C	7/ 8/78	5.0	55
D	7/ 8/78	16.5	170
E	7/ 8/78	5.0	60
F	7/ 8/78	3.0	22
G	8/ 3/78	12.0	125
H	8/ 3/78	6.0	23
I	7/ 8/78	6.0	45
J	7/ 8/78	5.0	30

SITE: P SPECIES: SP. AUROFRENATUM PHASE: IPH DATES: 7/ 8/78 TO 8/ 3/78



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SITE: M    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES:  1/ 8/78 TO  3/ 8/78
INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )
    1          1/ 8/78          ***                132
               2/ 8/78          ***                185

    2          2/ 8/78          ***                215
               1/ 8/78          ***                190

    3          1/ 8/78          ***                ***
               2/ 8/78          ***                159
               3/ 8/78          ***                ***

    5          1/ 8/78          ***                200
               2/ 8/78          ***                125

    6          1/ 8/78          ***                230
               3/ 8/78          ***                236

    7          2/ 8/78          ***                105
               2/ 8/78          ***                 34
               3/ 8/78          ***                241

    9          1/ 8/78          ***                 33
               1/ 8/78          ***                 88
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SITE: M    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES:  1/ 8/78 TO  3/ 8/78
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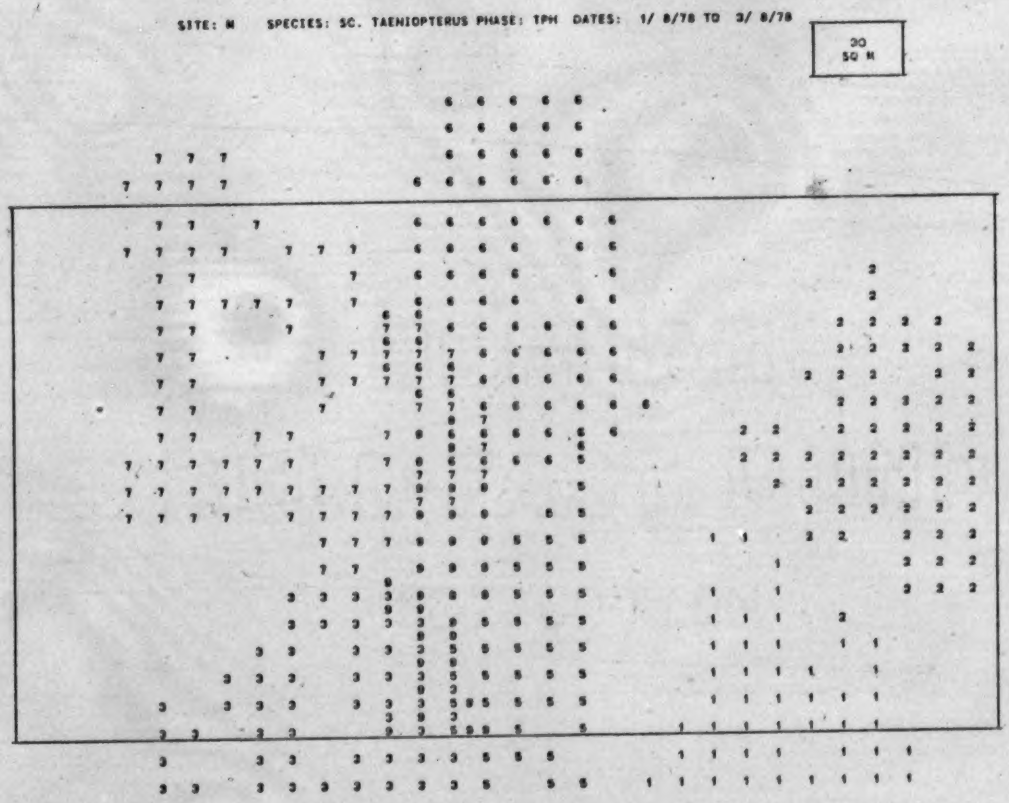

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SITE: M    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES: 10/ 1/79 TO 17/ 1/79

INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )

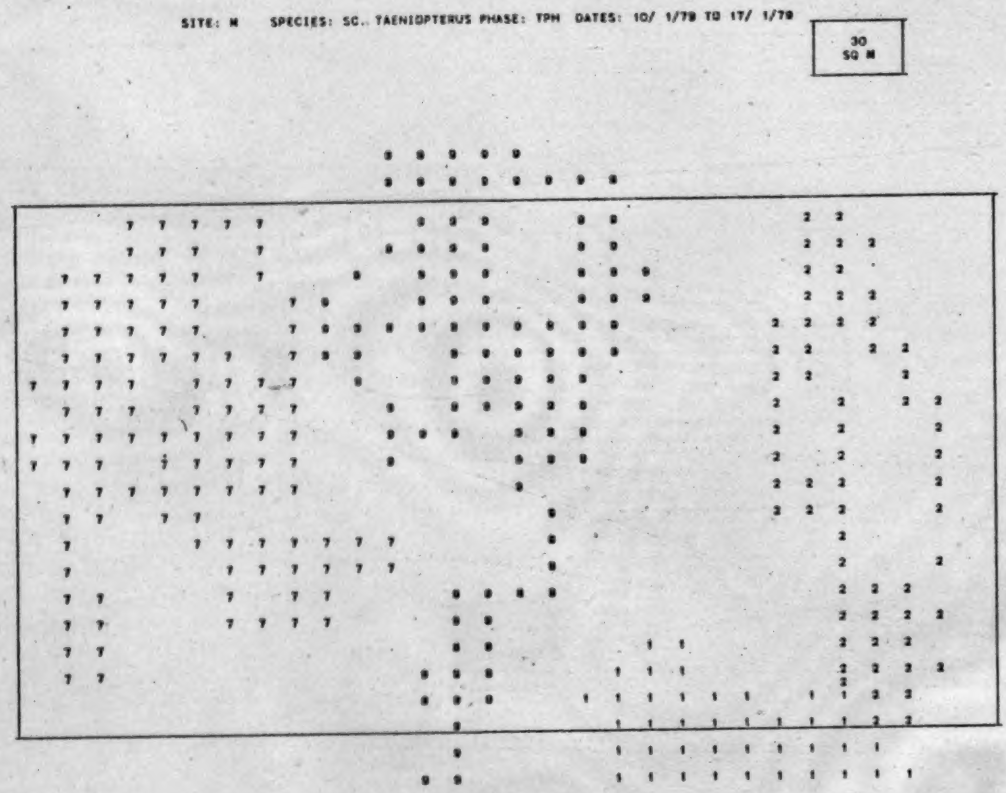
     1        12/ 1/79           15.5              87
              17/ 1/79           16.5             150

     2        10/ 1/79            8.0              69
              17/ 1/79           15.0             156

     7        11/ 1/79            6.0              28
              11/ 1/79            5.0              35
              15/ 1/79           17.5             342
              17/ 1/79           15.5             338

     9        11/ 1/79           12.5              95
              17/ 1/79           17.0             245
              17/ 1/79            4.0              98
```

SITE: M   SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 10/ 1/79 TO 17/ 1/79

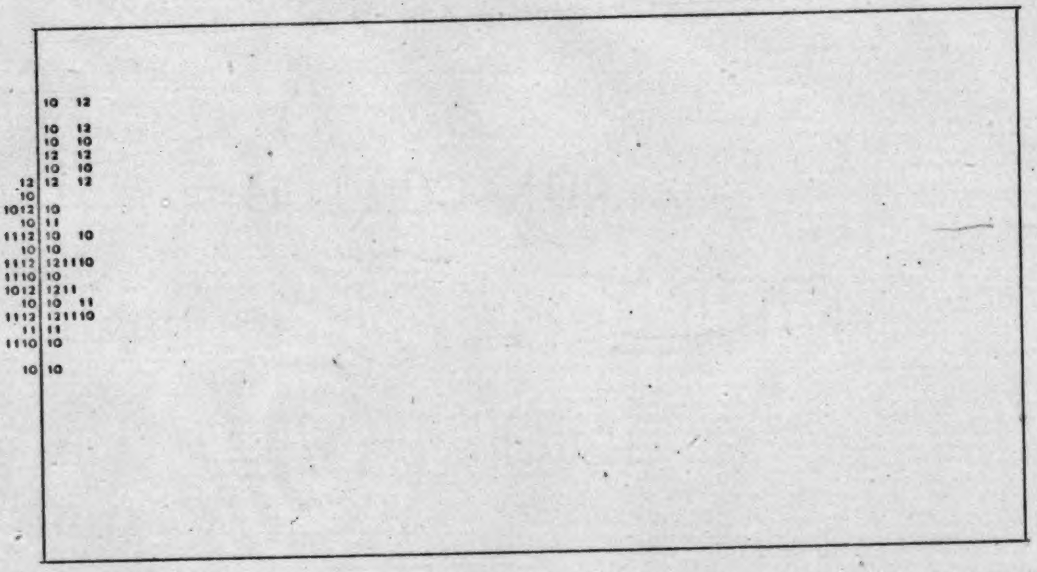


SITE: M SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 30/ 3/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
10	30/ 3/78	12.0	134
11	30/ 3/78	13.0	48
12	30/ 3/78	11.5	39

SITE: M SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 30/ 3/78

30
SQ M

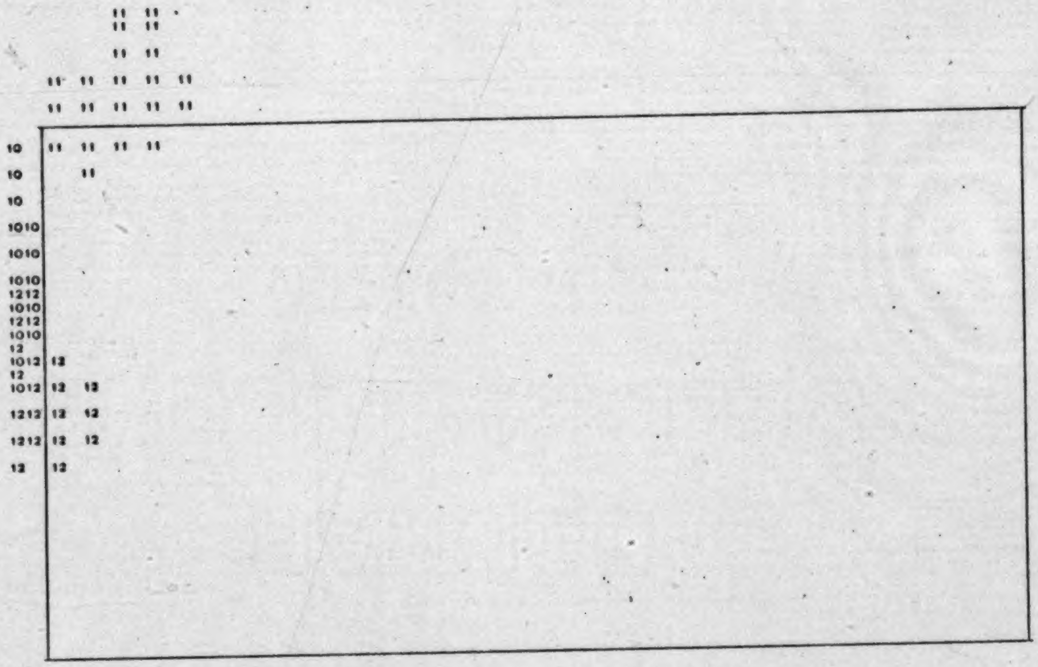


SITE: M SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 14/ 4/79 TO 20/ 4/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
10	14/ 4/79	15.0	97
11	20/ 4/79	19.0	55
12	14/ 4/79	15.0	95

SITE: M SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 14/ 4/78 TO 20/ 4/79

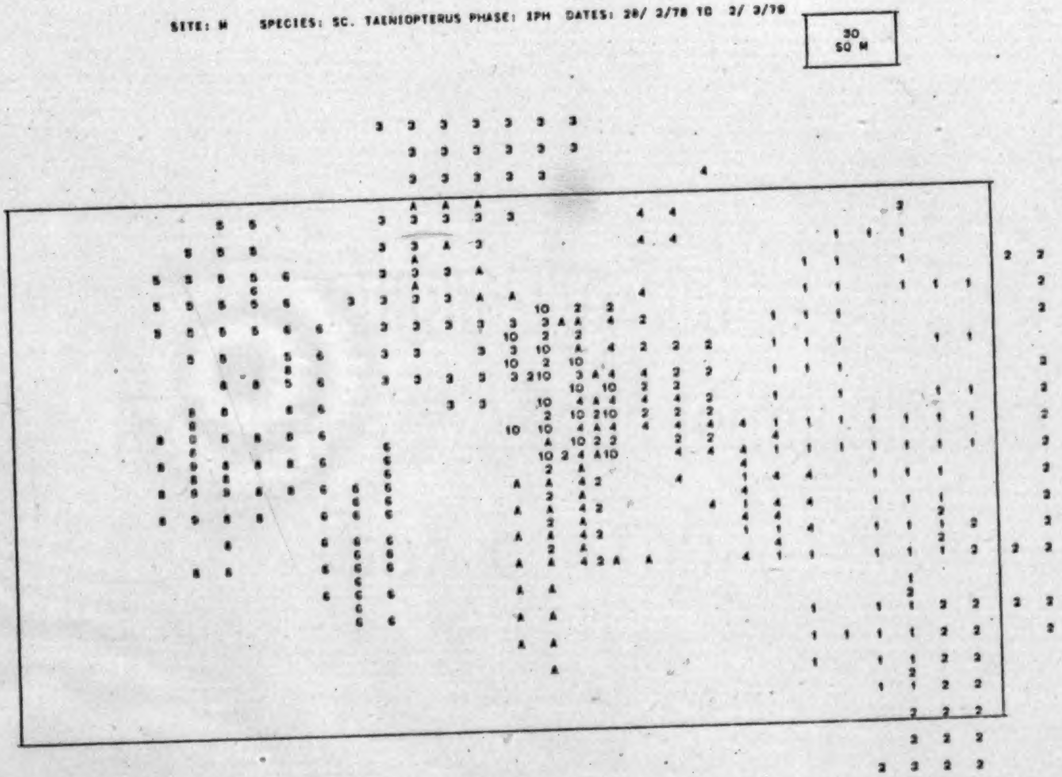
30
SQ M



SITE: M SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 28/ 2/78 TO 2/ 3/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	14/ 2/79	19.0	400
	15/ 2/79	15.0	115
2	16/ 2/79	17.0	210
	2/ 3/79	15.0	140
3	16/ 2/79	20.5	115
	19/ 2/79	20.0	257
4	19/ 2/79	11.5	74
5	19/ 2/79	10.0	27
6	19/ 2/79	10.0	27
	28/ 2/79	10.5	52
8	28/ 2/78	14.0	102
9	28/ 2/79	10.0	21
10	28/ 2/78	6.0	45
A	1/ 3/79	17.0	125

SITE: M SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 28/ 2/78 TO 2/ 3/79



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SITE: A    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES:  6/ 6/79 TO 11/ 6/79

INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )

     1        8/ 6/79            22.0               120
             10/ 6/79            20.0               130

     2        7/ 6/79            20.0                75
              8/ 6/79            20.0                80

     3        6/ 6/79            21.0               110
              7/ 6/79            20.0                65

     4        7/ 6/79            22.0               125
             11/ 6/79            20.0                40

     5        8/ 6/79            22.0               185
              9/ 6/79            23.0               125

     6        7/ 6/79            21.0                28
              8/ 6/79            20.0                35

     7        7/ 6/79            20.0               120
              8/ 6/79            20.0               125

     8        7/ 6/79            15.0                80
              8/ 6/79            15.0               105

     9        8/ 6/79            21.0               195
             11/ 6/79            20.0               170

    10        9/ 6/79            20.0               120
             10/ 6/79            15.0               130

     A        8/ 6/79            20.0                75

     B        9/ 6/79             5.0                35
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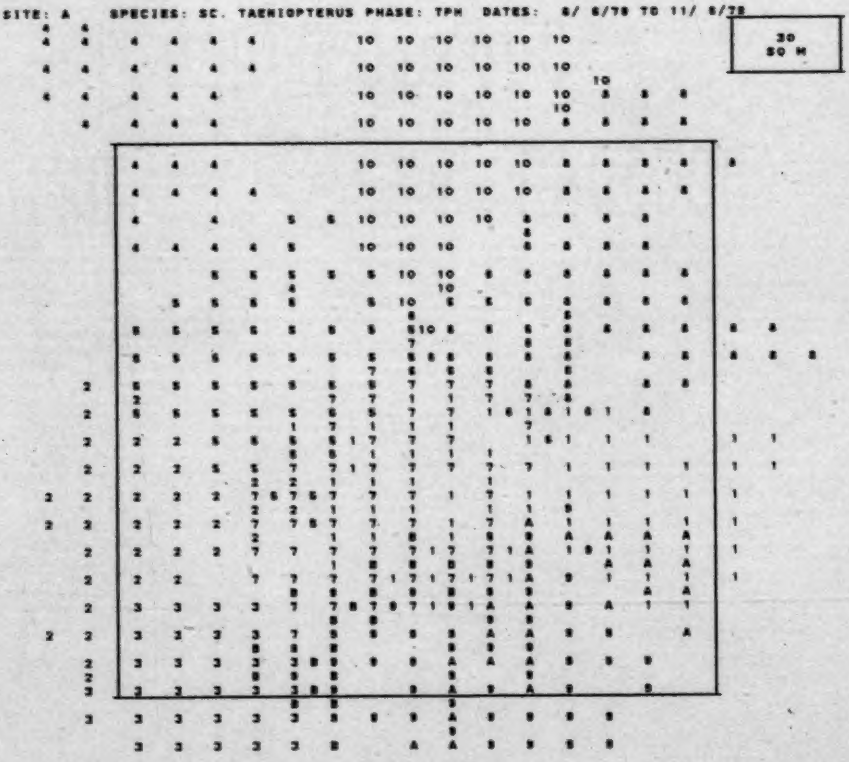
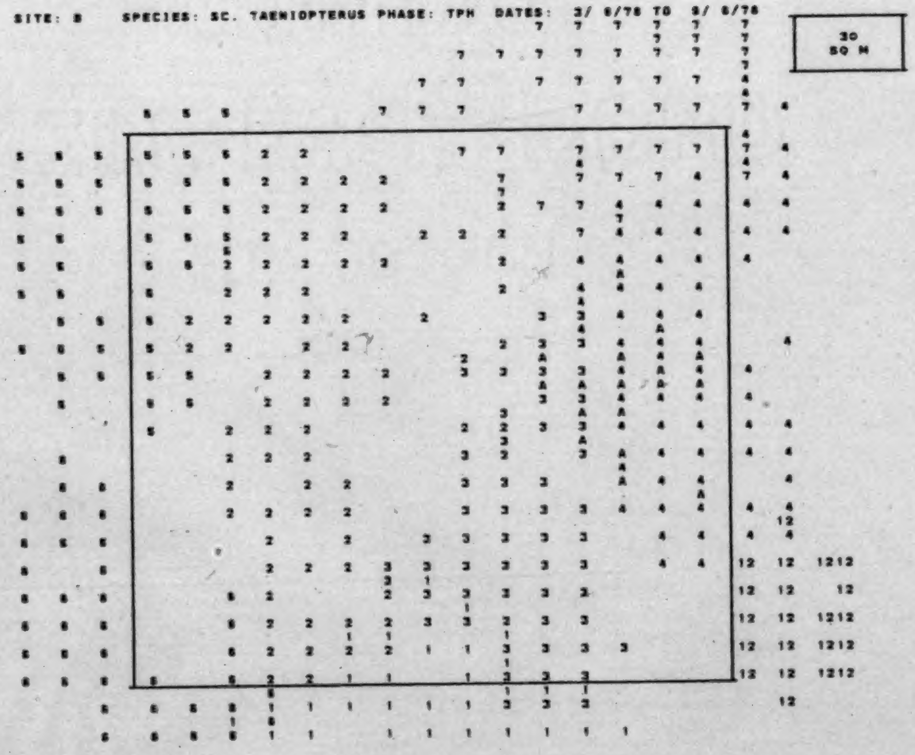
SITE: A    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES:  6/ 6/79 TO 11/ 6/79
```



SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 3/ 6/78 TO 6/ 6/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	3/ 6/78	16.5	***
	6/ 6/78	11.0	198
2	3/ 6/78	17.0	229
	5/ 6/78	16.5	308
3	3/ 6/78	13.5	263
	5/ 6/78	11.5	122
4	3/ 6/78	15.0	285
	5/ 6/78	14.5	253
	6/ 6/78	15.5	134
5	5/ 6/78	14.5	189
	6/ 6/78	15.0	213
6	5/ 6/78	15.5	144
	6/ 6/78	14.5	231
7	3/ 6/78	15.0	152
	6/ 6/78	16.0	348
12	6/ 6/78	15.0	155
A	5/ 6/78	5.0	72

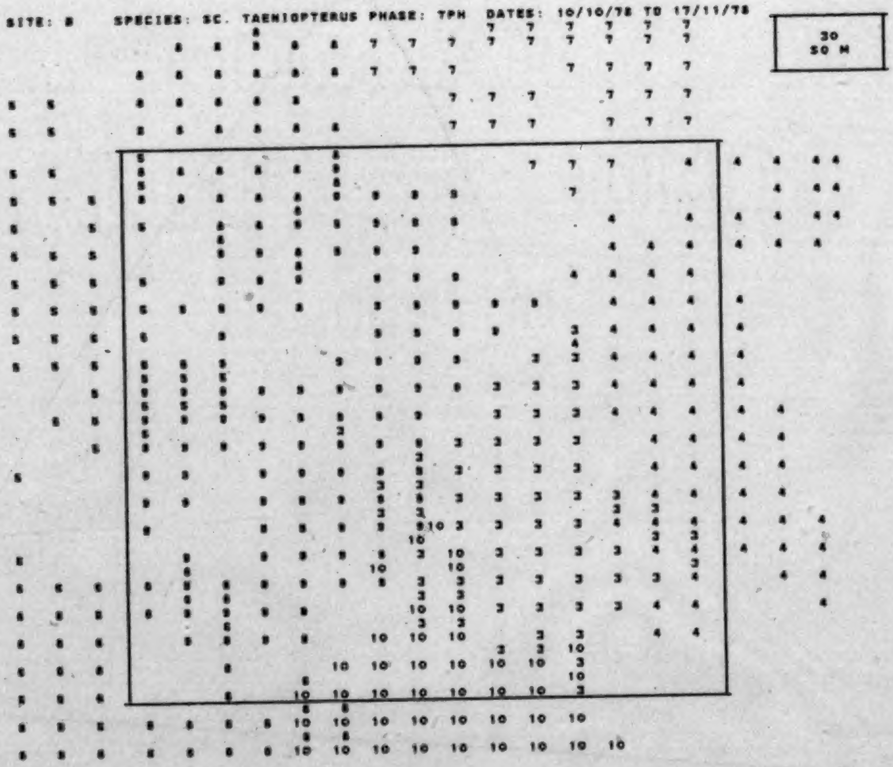
SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 3/ 6/78 TO 6/ 6/78



SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 10/10/78 TO 17/11/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
3	11/10/78	12.0	204
	13/11/78	20.0	245
4	10/10/78	16.5	282
	15/11/78	21.0	310
5	14/11/78	20.0	270
6	16/11/78	21.5	***
	17/11/78	15.0	212
7	17/11/78	20.0	***
8	14/11/78	20.0	230
	16/11/78	12.0	81
9	11/10/78	23.0	384
	13/11/78	20.0	370
10	12/10/78	15.0	148
	15/11/78	20.5	350

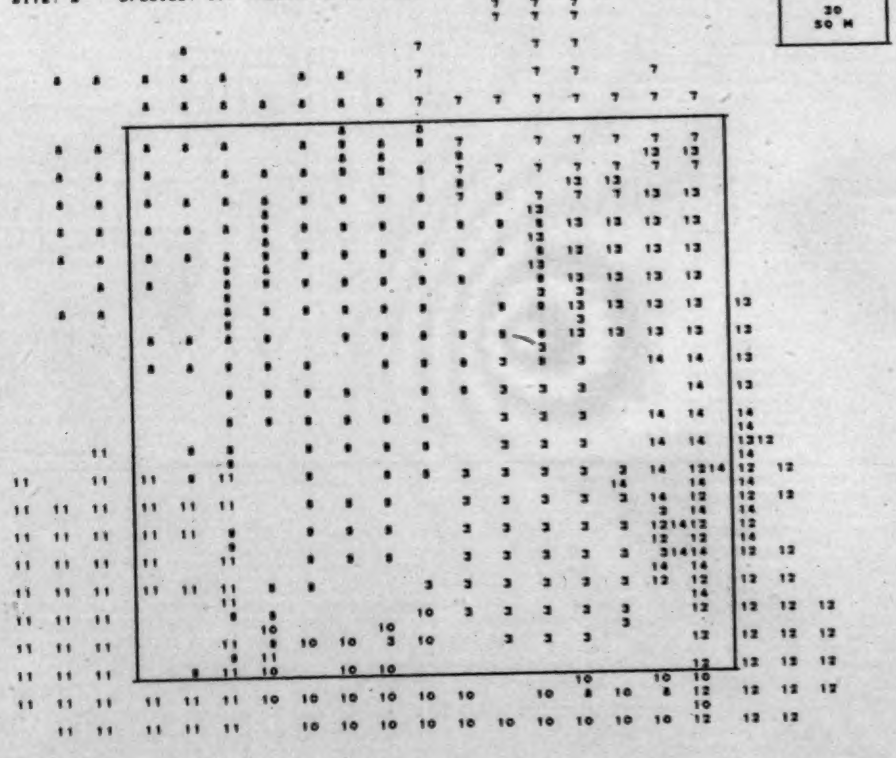
SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 10/10/78 TO 17/11/78



SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 9/ 5/79 TO 15/ 5/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
3	10/ 5/79	19.0	281
	13/ 5/79	16.0	43
7	9/ 5/79	15.0	210
8	11/ 5/79	15.0	280
	15/ 5/79	15.0	273
9	10/ 5/79	16.0	352
	11/ 5/79	15.0	539
10	11/ 5/79	17.0	***
	15/ 5/79	17.0	***
11	11/ 5/79	20.0	***
	15/ 5/79	20.0	***
12	10/ 5/79	15.0	151
	13/ 5/79	17.0	165
13	9/ 5/79	15.0	88
	13/ 5/79	16.0	143
14	13/ 5/79	15.0	100
	15/ 5/79	16.0	53

SITE: B SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 9/ 5/79 TO 15/ 5/79

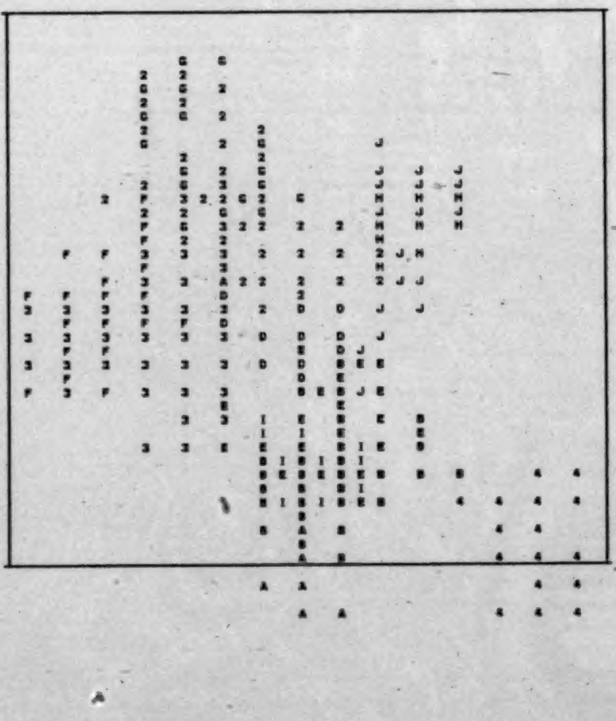


SITE: B SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 7/12/78 TO 12/12/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
2	11/12/78	5.0	52
	7/12/78	13.5	137
3	12/12/78	12.0	66
	11/12/78	10.5	120
4	11/12/78	10.0	92
A	11/12/78	4.5	38
B	12/12/78	13.0	40
	11/12/78	12.0	70
D	8/12/78	5.5	23
E	8/12/78	11.5	59
F	8/12/78	10.5	63
G	8/12/78	12.5	76
H	7/12/78	10.5	38
I	7/12/78	10.0	45
J	7/12/78	10.0	50

SITE: B SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 7/12/78 TO 12/12/78

30
SQ M



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SITE: P    SPECIES: SC. TAENIOPTERUS PHASE: TPH  DATES: 11/ 8/78 TO 14/ 8/78
INDIVIDUAL      DATE      MINUTES WATCHED    AREA ENCLOSED (SQ M )

     2        13/ 8/78           13.5              180
              13/ 8/78           15.0              180

     4        11/ 8/78           13.0              225
              11/ 8/78           20.0              485

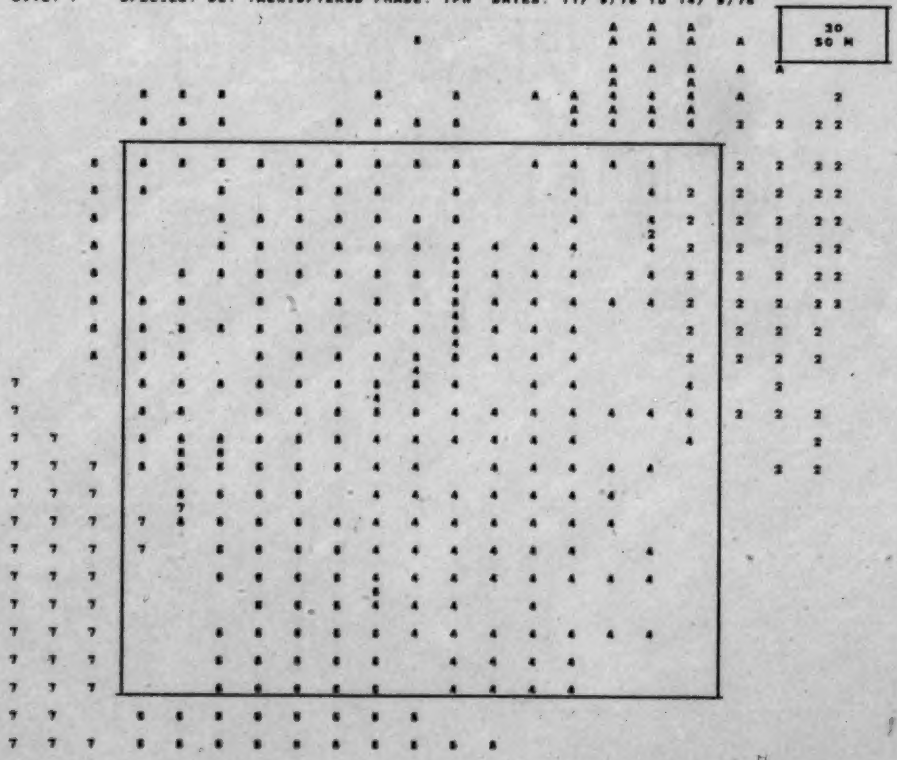
     6        13/ 8/78           21.0              320
              13/ 8/78           22.0              265

     7        14/ 8/78           18.0              180
              14/ 8/78           12.0              270

     8        11/ 8/78           17.5              380
              14/ 8/78           21.5              435

     A        13/ 8/78            8.0               60
```

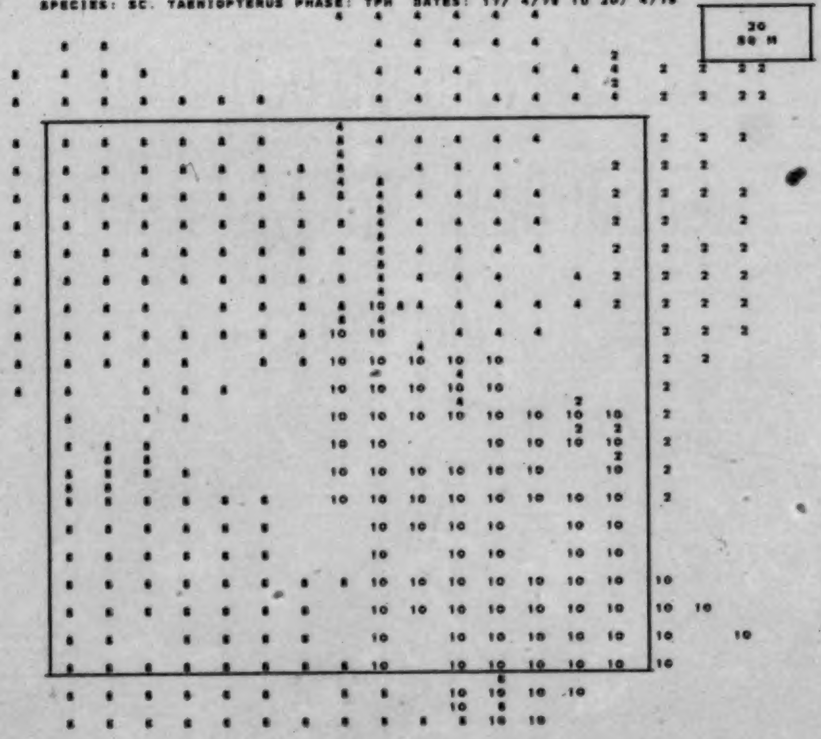
SITE: P   SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 11/ 8/78 TO 14/ 8/78



SITE: P SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 17/ 4/79 TO 20/ 4/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
2	19/ 4/79	15.0	120
	20/ 4/79	10.0	145
4	17/ 4/79	25.0	280
	19/ 4/79	15.0	215
6	18/ 4/79	25.0	380
	20/ 4/79	1[illegible].0	325
8	17/ 4/79	24.5	445
	19/ 4/79	18.0	340
10	18/ 4/79	20.0	350
	19/ 4/79	15.0	285

SITE: P SPECIES: SC. TAENIOPTERUS PHASE: TPH DATES: 17/ 4/79 TO 20/ 4/79

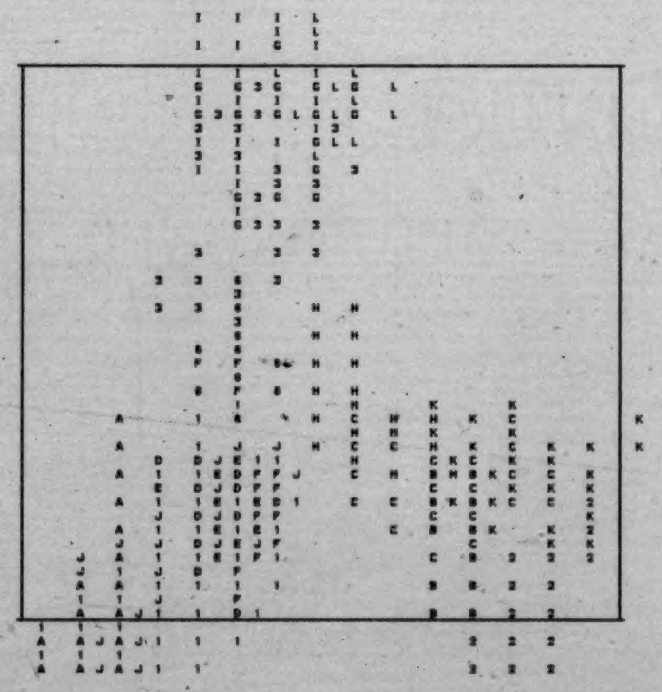


SITE: P   SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 14/ 9/78 TO 18/ 9/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	18/ 9/78 14/ 9/78 18/ 9/78	11.0 10.5 10.0	45 85 70
2	18/ 9/78	5.5	35
3	18/ 9/78	10.5	75
5	14/ 9/78	8.0	25
A	18/ 9/78	11.5	60
B	18/ 9/78	3.5	20
C	16/ 9/78	10.0	35
D	16/ 9/78	5.5	28
E	14/ 9/78	9.5	30
F	14/ 9/78	4.0	30
G	18/ 9/78	8.0	35
H	18/ 9/73	8,0	50
I	18/ 9/78	7.5	65
J	18/ 9/78	8.5	65
K	18/ 9/78	8.5	70
L	18/ 9/78	10.0	35

SITE: P   SPECIES: SC. TAENIOPTERUS PHASE: IPH DATES: 14/ 9/78 TO 18/ 9/78

30
SQ M



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SITE: M    SPECIES: SC. ISERTI       PHA.. TPH  DATES:  8/ 8/78 TO  8/ 8/78

INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )

    3         8/ 8/78            ***                83
              8/ 8/78            ***               144

    4         8/ 8/78            ***               ***
              8/ 8/78            ***               ***

   11         8/ 8/78            ***                55

   12         8/ 8/78            ***               158

   13         8/ 8/78            ***               132

    A         8/ 8/78            ***               ***

    B         8/ 8/78            ***                33
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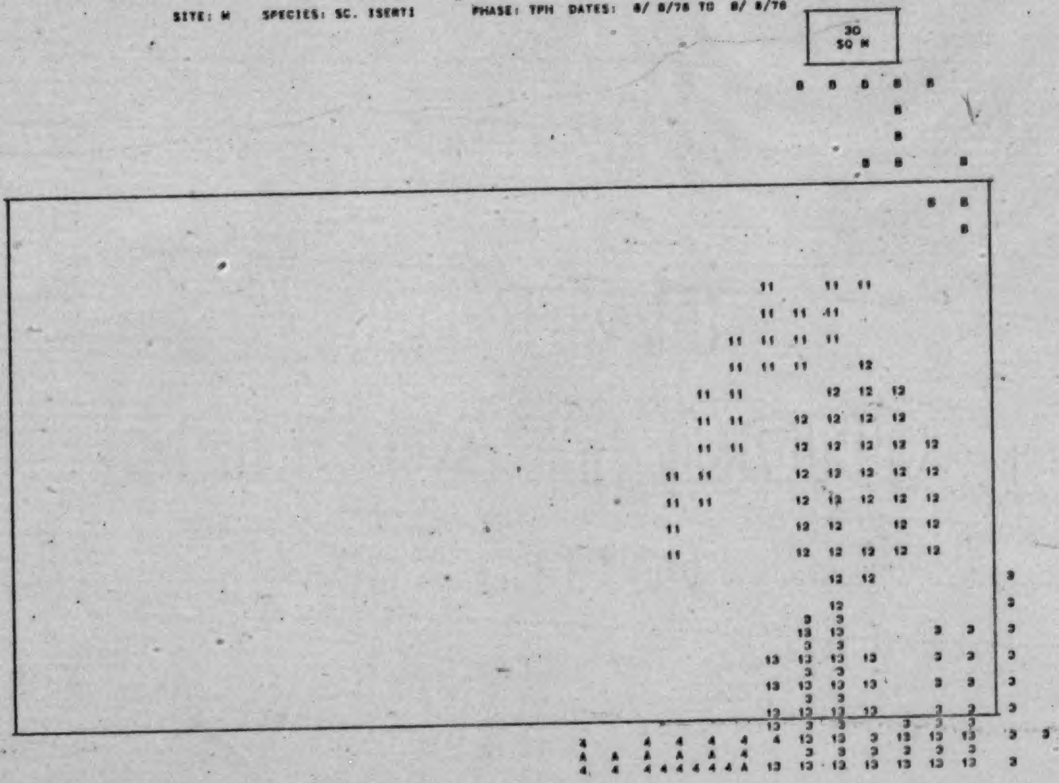
```
SITE: M    SPECIES: SC. ISERTI      PHASE: TPH  DATES:  8/ 8/78 TO  8/ 8/78
```



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SITE: M    SPECIES: SC. ISERTI        PHASE: TPH  DATES: 17/ 1/79 TO 15/ 2/79
INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )
     1        18/ 1/79           10.0                92
              17/ 1/79           10.0                80

     2        17/ 1/79           10.0                45

     3        15/ 2/79            4.0                35
              17/ 1/79           10.0                57

     4        19/ 1/79           11.0               150
              18/ 1/79           10.5                41

     5        30/ 1/79           10.0               140
              19/ 1/79           11.5                70
              18/ 1/79           10.0               169

     6        19/ 1/79           11.0                90

     7        18/ 1/79           10.0               ***
              18/ 1/79           10.0               ***

     8        18/ 1/79           11.0                86

     9        26/ 1/79            9.5               192

     A        18/ 1/79            3.5                26
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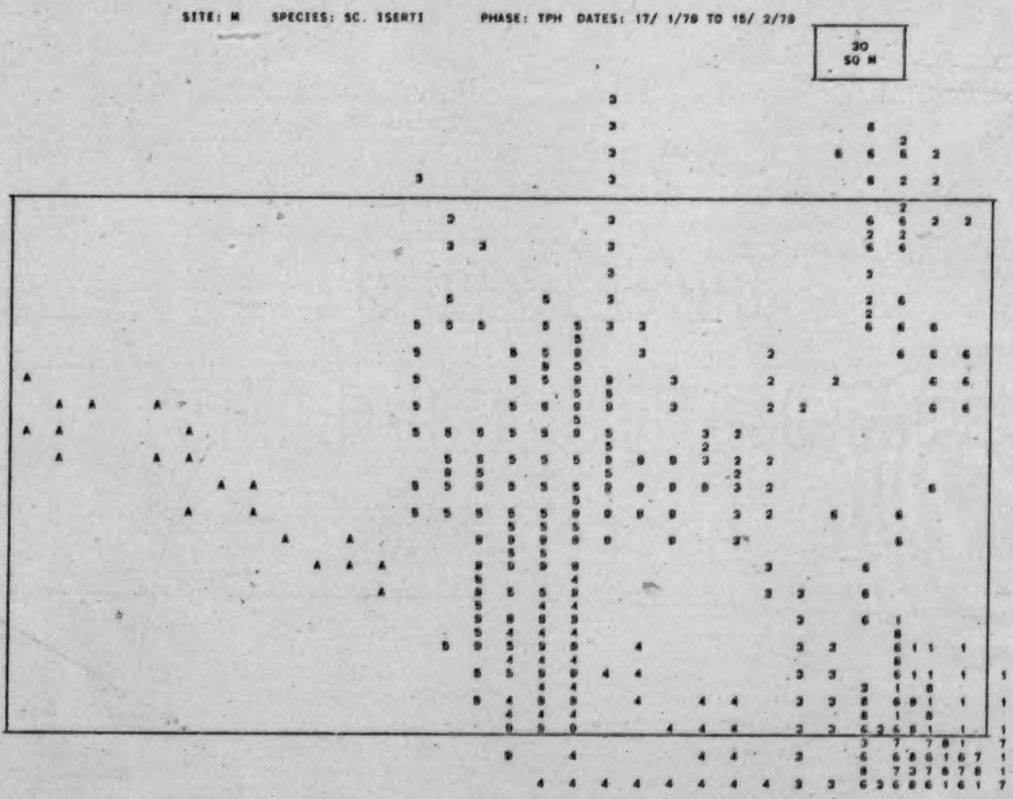
SITE: M    SPECIES: SC. ISERTI       PHASE: TPH  DATES: 17/ 1/79 TO 15/ 2/79
```



```
SITE: M   SPECIES: SC. ISERTI      PHASE: IPH  DATES:  1/ 3/79 TO  6/ 3/79
 INDIVIDUAL      DATE      MINUTES WATCHED    AREA ENCLOSED (SQ M )
     1          3/ 3/79         10.0                 26
                2/ 3/79         11.0                 30

     2          3/ 3/79         10.5                ***
                2/ 3/79         10.0                 38
                4/ 3/79         11.0                 15

     3          1/ 3/79         11.0                 18
                6/ 3/79          5.0                 41

     A          1/ 3/79         11.0                 48

     B          4/ 3/79         10.0                 18

     C          1/ 3/79         12.0                 82

     D          2/ 3/79         10.0                 30

     E          2/ 3/79          8.0                 48

     F          2/ 3/79         11.0                 85

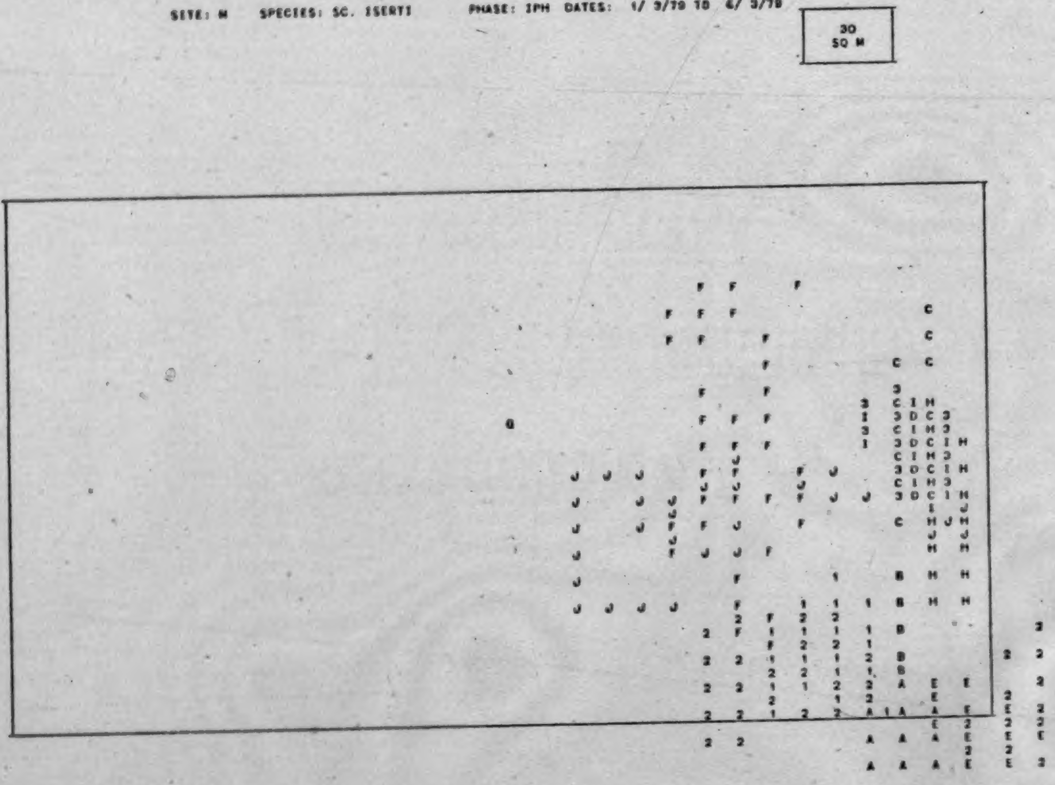
     G          3/ 3/79         11.0                  5

     H          5/ 3/79         10.0                 22

     I          5/ 3/79          8.0                 23

     J          5/ 3/79         10.0                 81
```

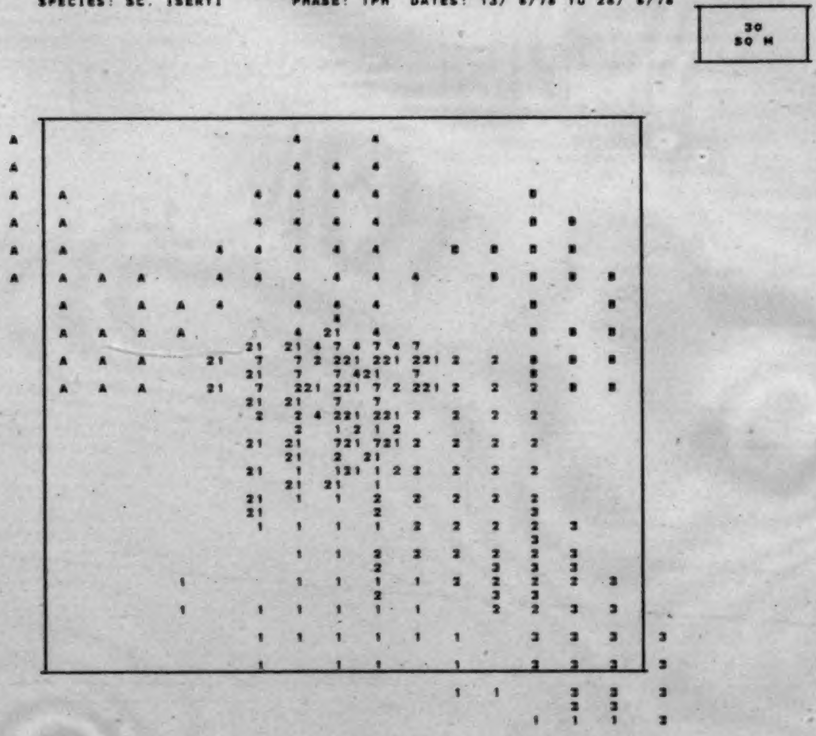
```
SITE: M   SPECIES: SC. ISERTI      PHASE: IPH  DATES:  1/ 3/79 TO  6/ 3/79
```



SITE: B   SPECIES: SC. ISERTI   PHASE: TPH DATES: 13/ 8/78 TO 28/ 8/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	13/ 8/78	11.0	86
	13/ 8/78	10.0	76
2	13/ 8/78	10.0	165
	18/ 8/78	10.0	84
	28/ 8/78	8.5	119
3	26/ 8/78	10.0	128
	27/ 8/78	10.0	125
4	26/ 8/78	10.0	98
	27/ 8/78	10.0	162
7	13/ 8/78	10.0	57
21	13/ 8/78	10.0	72
	15/ 8/78	13.0	95
A	25/ 8/78	10.0	107
B	28/ 8/78	***	128

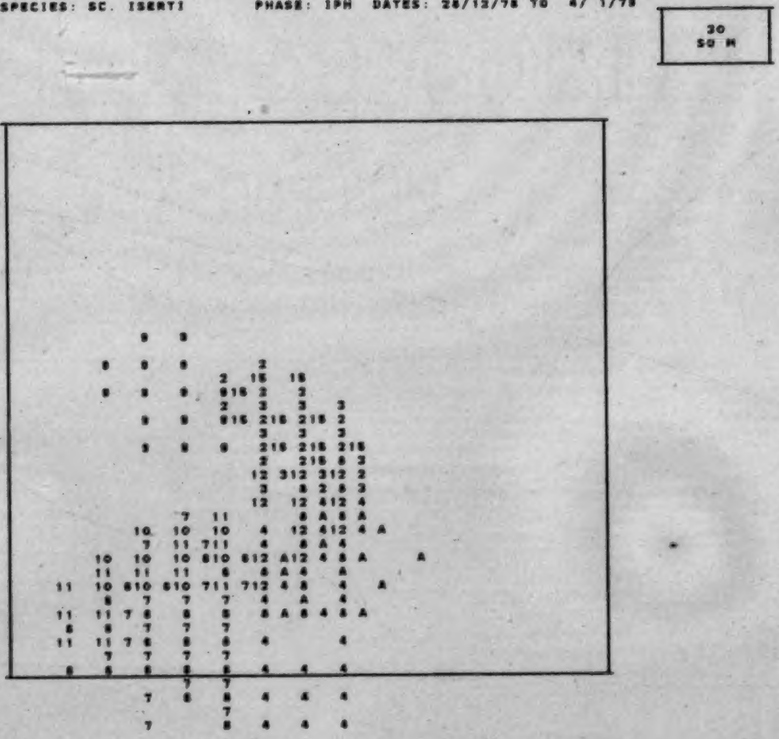
SITE: B   SPECIES: SC. ISERTI   PHASE: TPH DATES: 13/ 8/78 TO 28/ 8/78



SITE: B SPECIES: SC. ISERTI PHASE: IPH DATES: 28/12/78 TO 4/ 1/79

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
2	28/12/78	11.0	53
3	28/12/78	11.5	54
4	28/12/78	8.5	77
	28/12/78	6.0	65
6	28/12/78	10.5	75
7	28/12/78	10.0	50
8	28/12/78	5.5	32
9	4/ 1/79	9.0	66
10	4/ 1/79	6.0	27
11	4/ 1/79	7.0	28
12	4/ 1/79	5.5	31
15	28/12/78	10.0	31
A	28/12/78	5.0	60

SITE: B SPECIES: SC. ISERTI PHASE: IPH DATES: 28/12/78 TO 4/ 1/79



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SITE: B    SPECIES: SC. ISERTI        PHASE: TPH  DATES: 13/12/78 TO 28/12/78

INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (SQ M )

     5        20/12/78            10.0              88
              13/12/78            10.0             159

     6        27/12/78            12.0             ***
              27/12/78            12.0             ***
              27/12/78            11.0             122

     7        27/12/78            10.0             109
              20/12/78             7.5              88

     8        28/12/78            10.0              75
              27/12/78            10.0             ***

     9        28/12/78            10.0              25
              27/12/78            10.0              88

    10        28/12/78            10.0             103
              28/12/78            10.0              75

    11        28/12/78            11.0              70
              28/12/78            10.0              71

     A        20/12/78             2.0             ***
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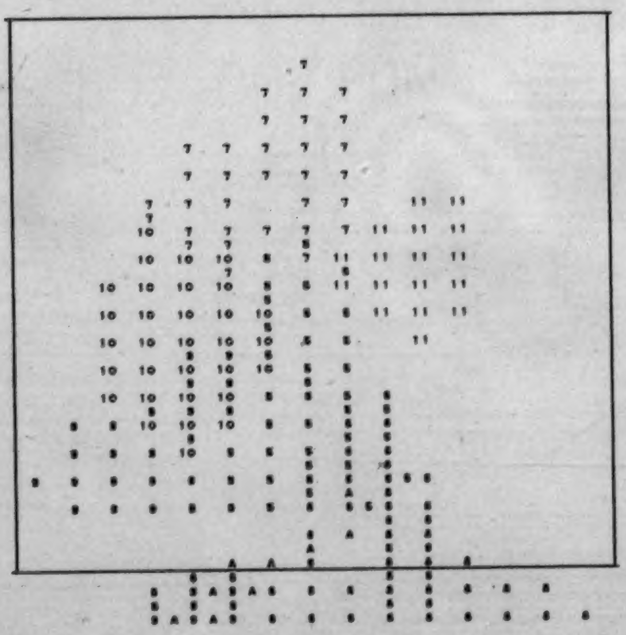
SITE: B    SPECIES: SC. ISERTI        PHASE: TPH  DATES: 13/12/78 TO 28/12/78
```

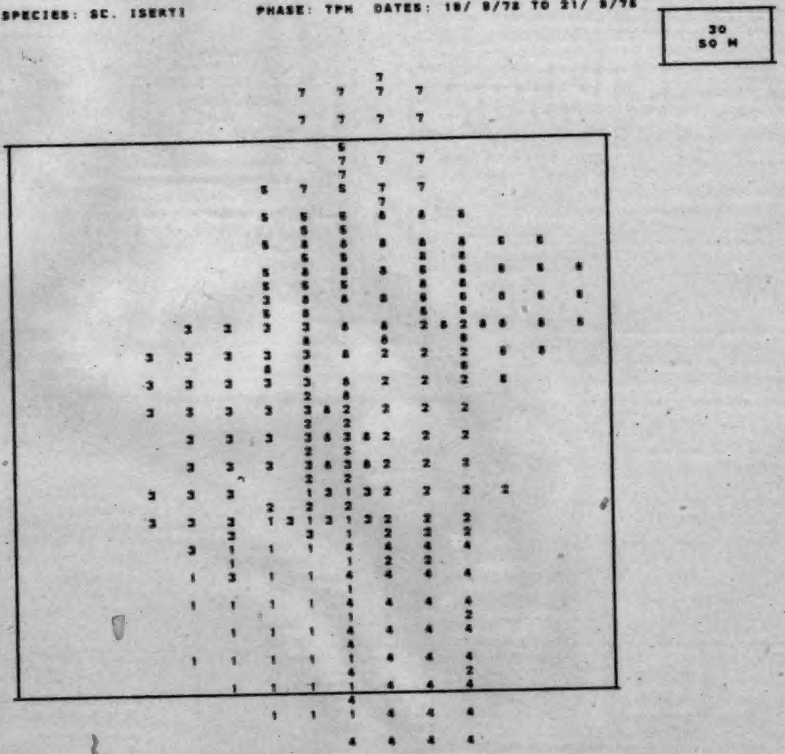
30
SQ M



SITE: P SPECIES: SC. ISERTI PHASE: TPH DATES: 19/ 9/78 TO 21/ 9/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
1	19/ 9/78	12.0	118
	20/ 9/78	10.0	93
2	19/ 9/78	10.0	108
	20/ 9/78	11.0	88
3	19/ 9/78	7.5	88
	20/ 9/78	10.0	128
4	19/ 9/78	10.5	88
	20/ 9/78	11.0	88
5	21/ 9/78	10.5	45
	20/ 9/78	10.0	45
6	20/ 9/78	10.5	70
	21/ 9/78	10.0	50
7	20/ 9/78	5.5	55
	21/ 9/78	8.5	45
8	20/ 9/78	10.0	80
	21/ 9/78	12.0	85

SITE: P SPECIES: SC. ISERTI PHASE: TPH DATES: 19/ 9/78 TO 21/ 9/78



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SITE: P    SPECIES: SC. ISERTI        PHASE: TPH  DATES: 24/ 4/78 TO 28/ 4/78
INDIVIDUAL      DATE       MINUTES WATCHED    AREA ENCLOSED (30 M )

     2        27/ 4/78            9.0               83
              28/ 4/78           10.0               53

     5        27/ 4/78           15.0              100
              28/ 4/78           11.0              148

     9        24/ 4/78           15.0              103
              27/ 4/78           10.0               85

    10        24/ 4/78           12.0               38
              28/ 4/78           11.0               48

    11        28/ 4/78            5.0               45
              24/ 4/78           15.0               85

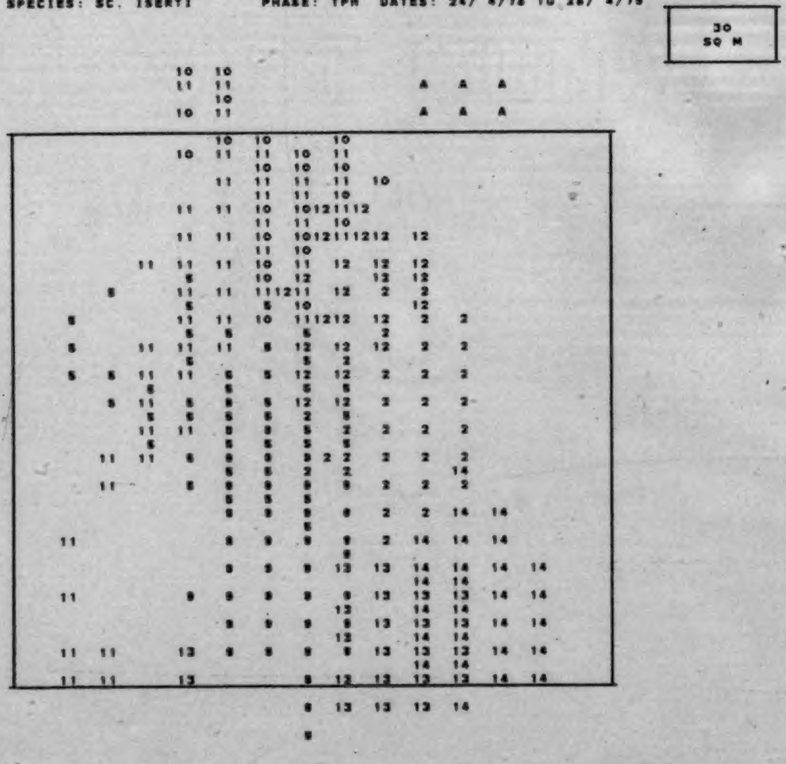
    12        27/ 4/78           15.0               53
              28/ 4/78           10.0               38

    13        28/ 4/78           10.0               63
              27/ 4/78           10.0               58

    14        27/ 4/78            9.0               80
              28/ 4/78           11.0               78

     A        27/ 4/78           10.0               28
```

```
SITE: P    SPECIES: SC. ISERTI        PHASE: TPH  DATES: 24/ 4/78 TO 28/ 4/78
```



SITE: P SPECIES: SC. ISERTI PHASE: IPH DATES: 23/ 9/78 TO 25/ 9/78

INDIVIDUAL	DATE	MINUTES WATCHED	AREA ENCLOSED (SQ M)
A	23/ 9/78	6.0	55
B	23/ 9/78	5.0	30
C	23/ 9/78	8.5	50
D	23/ 9/78	14.0	41
E	25/ 9/78	11.0	35
F	25/ 9/78	8.0	60
G	25/ 9/78	10.0	48
H	25/ 9/78	10.0	55
I	25/ 9/78	9.0	30
J	25/ 9/78	10.0	43
K	25/ 9/78	10.0	45
L	25/ 9/78	10.0	65
M	25/ 9/78	10.0	30
N	25/ 9/78	6.0	48

SITE: P SPECIES: SC. ISERTI PHASE: IPH DATES: 23/ 9/78 TO 25/ 9/78